Gerhard Ernst Overbeck
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South Brazilian Grasslands

Ecology and Conservation of the *Campos Sulinos*

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Part I
Introduction

Chapter 1
The *Campos Sulinos*: Introduction to the Book

Gerhard Ernst Overbeck, Glayson A. Bencke, Sandra C. Müller, and Valério D. Pillar

1.1 The *Campos Sulinos*: Continued Neglect in Conservation

When thinking of Brazil, the most biodiverse country of the planet, most people intuitively look up to find its biodiversity – both on a map, where the Amazon is depicted in the north, or in vegetation, where people tend to focus on the trees and the forests. How curious it thus seems that we have to look down to the south and to the grasslands that rise only little above the ground to get a full picture of Brazil's rich biological heritage. Who is aware of the fact that the record for the number of plant species on 1 m^2 is held by the South Brazilian grasslands (da Silva Menezes et al. 2018), or that the Pampa region alone holds more than 12,500 species of plants, animals, and fungi (Andrade et al. 2023a)? The *Campos Sulinos*, as the South Brazilian grasslands are called in Portuguese, hold an extraordinary biodiversity, but this is not well known in the general public and even in the Brazilian or international community of biodiversity researchers, nor recognized in conservation.

Already in a 2007 article, the South Brazilian grasslands were called 'Brazil's neglected biome' (Overbeck et al. 2007) because of their poor consideration both in science and in conservation. Back then, they in fact still were very poorly regarded

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in ecological research and even less in conservation. Symptomatic of this situation, at the time Brazil's main law of nature conservation still was the "Forest Code". Since then, the scenario has changed regarding research that – as well evidenced by the contribution in this volume – clearly has much increased. The *Campos Sulinos* definitely have become an interesting subject for science, even if – this is also documented in many chapters in this volume – many knowledge gaps and research needs remain. When we turn to conservation, the situation is different. The scientific treatment of conservation questions certainly has increased, often pointing out conservation needs. However, implementation of conservation has not advanced at a sufficient pace to respond to the anthropogenic pressures the region faces. On the contrary, the entire region has seen, and continues to see, a continuous loss of natural vegetation, and especially of grasslands, besides other conservation problems, like widespread occurrence of invasive species and the foreseeable effects of climate change. At the same time, the cover of protected areas is very low.

As much as southern Brazil was not much considered by the Portuguese in the first period of Brazil's colonial history, they still appear to be rather marginal in the country's conservation debate. Clearly, the South Brazilian grasslands suffer from 'Biome Awareness Disparity' (Silveira et al. 2022), a recently diagnosed global problem for grassy ecosystems that adds to prior evidence on the neglect of grassy ecosystems worldwide (Bond and Parr 2010; Veldman et al. 2015). In Brazil, in particular, this 'forest bias' in conservation remains evident, both in public debate and in policy. Needless to say, Brazil's biodiverse tropical forests need all possible attention in conservation and sustainable development. For the Amazon, this is underlined by the regions' significance for global climate, and for the Atlantic Forest by the historically severe degradation that requires extended restoration action, not only because of high biodiversity, but also to secure the quality of life of human populations in this densely populated region. But this attention should not go at the expense of Brazil's diverse grasslands and savannas that span over 27% of the country's territory, have an amazing biodiversity and provide important ecosystem services to human populations (Overbeck et al. 2022). One of these systems are the South Brazilian grasslands.

1.2 A Brief Guide Through Terminology for the *Campos Sulinos*

The South Brazilian grasslands are clearly defined in the very term: they are the grasslands that are located in the southern region of Brazil, i.e., in the three southern states Rio Grande do Sul (RS), Santa Catarina (SC), and Paraná (PR) (Fig. 1.1). The *Campos Sulinos* span across a very heterogeneous region. They are part of two different biogeographic provinces, the Parana and Pampean provinces (Cabrera and Willink 1980) that correspond to two ecoregions and even biomes of the much-used classification by Olson et al. (2002). The southern part, corresponding to the Pampean province, is part of the "Uruguayan savanna" (a somewhat misleading

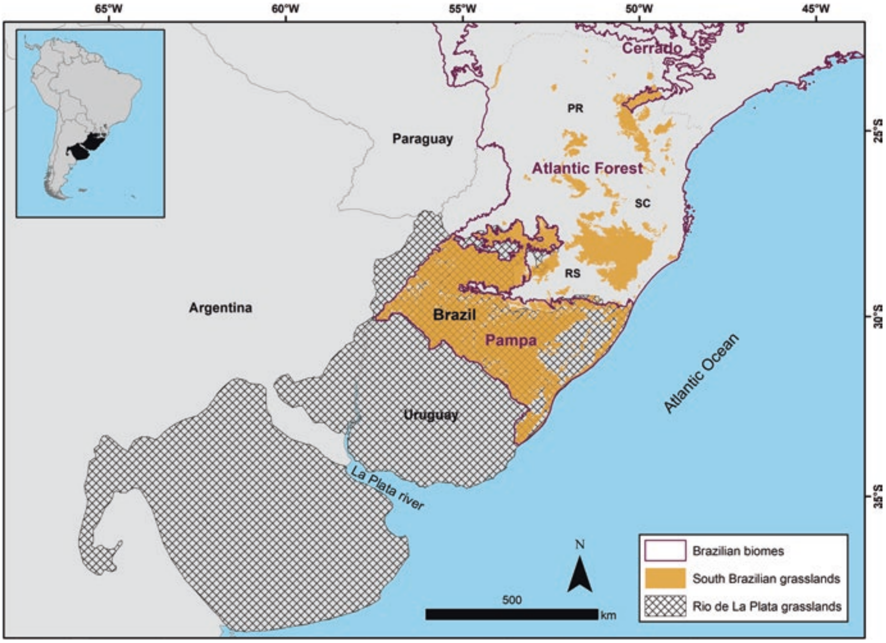

Fig. 1.1 Extension of the South Brazilian grasslands (*Campos Sulinos*) across southern Brazil. In orange, the original extension of South Brazilian grasslands, based on IBGE (2019) data (see Overbeck et al. 2022 for details). The southern part of the *Campos Sulinos* is located within the Brazilian Pampa region (or biome, according to the IBGE classification), which corresponds to the Brazilian part of the Rio de la Plata Grassland region (*Pastizales del Río de la Plata*; Soriano et al. 1991; Andrade et al. 2019), the large region dominated by grasslands in southeastern South America. The *Campos Sulinos* located to the North of the Pampa are part of the Atlantic Forest region (or biome, according to the IBGE classification). (Map by Eduardo Vélez-Martin)

term, given that part of the region is in Brazil, and climate is not a savanna climate). These 'Uruguayan savannas', comprising the southern part of RS and Uruguay, are part of the *Pastizales del Río de la Plata* region (Soriano et al. 1991; Andrade et al. 2019; Fig. 1.1), i.e., the extended area of temperate to subtropical grasslands that span around the Río de la Plata in southeastern South America. The term *Pastizales* (Spanish for 'grazing lands') clearly indicates the dominant land use in the region: these grasslands are used for grazing, and have been so from the seventeenth century on after cattle was introduced by European settlers. The northern part of the *Campos Sulinos* is located within the Atlantic forest ecoregion, specifically within the Araucaria Moist forests (Olson et al. 2002). This means that the region we call *Campos Sulinos* includes grassland areas within two different major biomes: the southern portion is part of the 'Tropical and subtropical savannas, grasslands and shrublands' biome, while the grassland enclaves in the northern portion are part of the 'Tropical rainforest biome' (Olson et al. 2002). Brazil has its own regional biome classification (IBGE 2019) where the term 'biome' is used in a somehow different way than in the international debate; in this classification, the *Campos*

Sulinos belong to the 'Pampa' (in the South) and to the 'Atlantic Forest' (in the North) biome, corresponding to the major biomes and biogeographical provinces mentioned above.

When we use the term *Campos Sulinos* we thus refer to a large region predominantly covered by grassy environments that include, in the South, grasslands that are situated in grassland-dominated landscapes, and, in the North, grasslands that are, more or less, enclaves in forest landscapes. While these two major regions of grassland display many similarities in terms of their ecology and also their land use and associated cultural practice (livestock raising), they also present differences in relation to their biogeography and dynamics. This means that researchers working with grasslands in southern Brazil may, in many cases, use the *Campos Sulinos* region as presented here for their study, but in some specific cases, for example, in phylogeographic analyses (Baez-Lizarazo et al. 2023, Chap. 5 in this volume) the region of the *Pastizales del Río de la Plata* is more appropriate. While the majority of chapters in this book focuses on the *Campos Sulinos* region, there are exceptions; in part, this also reflects availability of data and thus points out research needs so that in the future integrated studies across the *Campos Sulinos* region as a whole will be possible.

1.3 Land Use Change in the *Campos Sulinos* and Impacts

Land use change has strongly affected the region and its natural environments. Anthropogenic use, mostly for agricultural production today is the most prominent land cover class, and in the past decades grasslands have been the ecosystem type with the highest rate of loss (Fig. 1.2). Land use change continues at a fast pace (Azevedo et al. 2023). The effects of conversion of natural landscapes on biodiversity and ecosystem services in general are well known from many regions of the world. In the *Campos Sulinos*, land use change leads to biodiversity losses (discussed in detail in several chapters of this book) and transformation of a landscape with an enormous cultural significance. The grasslands in the region are the basis for the *Gaúcho* culture and have been, since the introduction of cattle by Europeans in the seventeenth century, an important basis for the regional economy. The diversity of forage species in the South Brazilian grasslands is remarkable, and the specific climatic conditions of the region lead to unique plant communities where winter C3 and summer C4 grasses coexist, which translates into a high potential for cattle raising in the region (Nabinger et al. 2000). Indeed, we can say that the *Campos Sulinos* have a vocation for livestock production based on natural grasslands, and, as we will see later in this book, grazing by domestic cattle is a way to preserve the natural biodiversity of this region. Halting land use change and implementing biodiversity- and carbon-friendly strategies of land management are important steps to achieve Brazil's commitment to global conservation and climate change mitigation goals. However, given the current state of conservation in the region, this does not seem to be a goal to be reached easily.

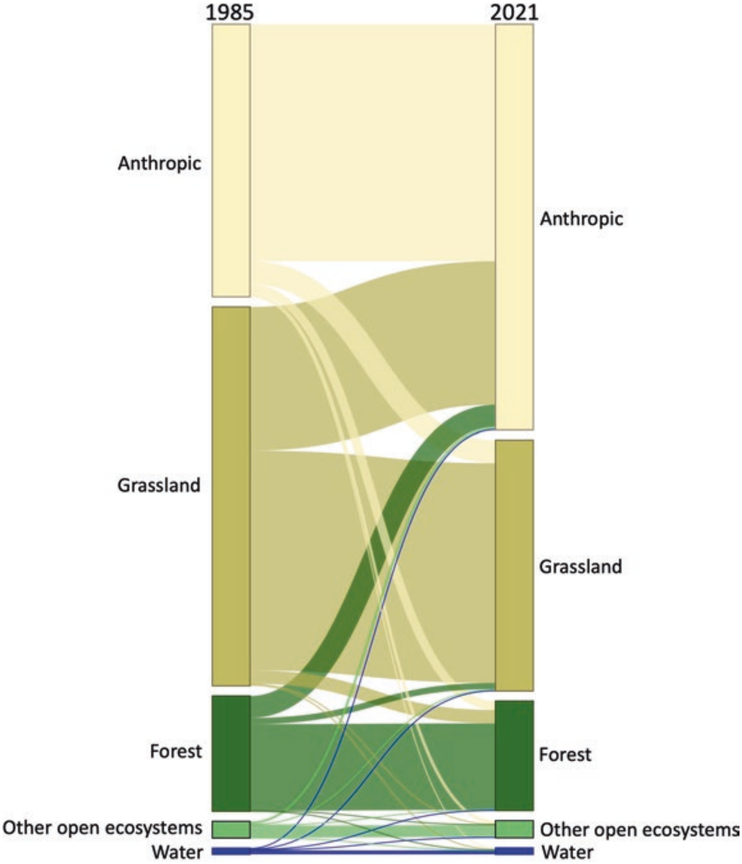

Fig. 1.2 Land use change in the *Campos Sulinos* region (as defined in Fig. 1.1) from 1985 to 2021. (Figure by E. Vélez-Martin (from Chap. 17 in this volume))

1.4 Content of This Book

In this book, we provide a synthesis of current knowledge on ecology, biodiversity, and conservation of the *Campos Sulinos* region. The book is structured into four parts. Part I serves to settle the scene, by presenting information about geology, geomorphology, climate, and ecosystem history, information necessary to understand biodiversity patterns. In Part II, we delve into the ecology and biodiversity of the region, with information about different types of ecosystems and groups of organisms, describing their main characteristics, natural dynamics, but also conservation threats. In Part III, we step out of the grasslands and into shaded environments: the focus here is on the forest–grassland interface and on the forests that share the space with grasslands in parts of the region. Finally, in Part IV, we focus explicitly on conservation-related questions, with the aim to give a general picture on land use change, on conservation of grasslands in protected areas, on invasive species and their management, and on the more recent debate on grassland restoration.

Part I begins with a chapter on geodiversity and geological memories of the southeastern region of the South American plate where we today find the *Campos Sulinos*. The contribution by Menegat (2023) gives a vivid description of the evolution of continents, the fragmentation of Gondwana in current South America and the following periods that led to today's geomorphological configuration of the region, ending with the recent formation of the South Brazilian coastal plain in the Quaternary. In the following chapter, Stock da Rosa et al. (2023) likewise take a look into the past, this time with a focus on fossil-bearing rocks, taking the reader to a journey through the Permian, Triassic, Jurassic-Cretaceous periods, and the Pleistocene Epoch. The fossil records of the region are remarkable, and, evidently, this knowledge has direct relevance for the understanding of today's ecosystems, e.g., through plant adaptations that evolved in response to the presence of large grazing animals. Behling et al. (2023) illustrate, based on the interpretation of paleopollen samples conserved in peat profiles, the more recent vegetation history in the region, thus telling the story of the South Brazilian landscapes over the past 40,000 years. This knowledge of past vegetation history has clear relevance for conservation questions discussed later on, as it indicates that both fire and grazing shaped landscapes in the past. Then, Baez-Linarazo et al. (2023) present a comprehensive overview of the angiosperm historical biogeography in the region known as *Pastizales del Rio de la Plata* and neighboring regions, by integrating a comprehensive phylogeny with over 70,000 plant species. For this chapter with a biogeographical focus, this great ecoregion that corresponds to the Pampean province was the more appropriate study region. Their analyses show that the Pampa is a macroevolutionary sink of angiosperm diversity, with a strong asymmetry of lineage exchange from other areas to the region, in recent geological times. In the following chapter, Hasenack et al. (2023) take us to the present and give a didactic overview on the current climatic and edaphic conditions of the region. They illustrate the climatic gradients we find in the region and discuss the consequences of El Niño Southern Oscillation events. Further, they provide a functional and regionalized description of soils in the region and discuss consequences for vegetation patterns. The chapter also includes a brief debate on the expected effects of climate change. In the last contribution in this first section of the book, Golin (2023) sheds light on the history of indigenous people that inhabited the region before the arrival of European colonizers and describes both the organization of these populations during colonial times and the many violent conflicts that led to the tragic extermination of indigenous populations in southern Brazil whose legacy, however, continues in cultural practices in the region until today.

In Part II, we take a closer look at the biodiversity and ecological characteristics of the *Campos Sulinos*. The section starts with the chapter by Andrade et al. (2023b) on grassland vegetation. While information on floristics and different types of grassland is initially presented in a concise way, the focus of the chapter lies on the drivers of grassland dynamics, in particular on the disturbances that shape these systems.

The chapter presents plant adaptations and vegetation responses to fire and grazing and discusses consequences for vegetation management and conservation. In the following chapter, Turchetto et al. (2023) investigate a different facet of grassland diversity: they present information on the genetic structure of plant populations and thus evidence for microevolutionary processes, using plant genera that originated in the region, mainly *Petunia* and *Calibrachoa* that are particularly well studied. Based on their data, they also discuss consequences for biodiversity conservation in the region where genetic aspects still are little considered. Bencke et al. (2023) present a comprehensive overview of the birds that inhabit the open ecosystems of the *Campos Sulinos*. Drawing from a compilation of literature and extensive personal knowledge, they explore different aspects related to the life history and conservation of birds in southern Brazil. The region holds a high number of grassland specialists and also is of high importance for many migratory birds. The chapter includes many links to vegetation, and specifically discusses the relation of different groups of birds to grassland management. Hartz et al. (2023) present a synthesis of knowledge on the 134 native mammal species that occur in the *Campos Sulinos*. They not only describe the different species groups and important representatives, but also discuss specific adaptations to live in open habitats. Further, they describe the importance of mammals for the ecosystems they occur in, e.g., by providing important ecosystem services (e.g., pollination by bats, primates as sentinels for the yellow fever virus) and consequences for conservation. Becker et al. (2023) take us into a journey to the freshwater environments of the *Campos Sulinos*: they give insights into the diverse fish fauna of the region that hosts 570 fish species and has a high level of endemism. A high proportion of these species is endangered, and protection levels are insufficient. The chapter provides evidence of the effects of land use changes on fish populations and discusses consequences in conservation. Maltchik et al. (2023) keep us in environments with a high relevance of water: they present a synthesis on the ecology and conservation state of wetlands in the region. Starting with the drivers of wetland biodiversity, including effects of land management and dispersal processes, they provide us with the scientific basis for a better conservation of wetlands, a still too often overlooked component of biodiversity with a high relevance for hydrological processes on the landscape scale. Wetlands provide important ecosystem services, and so do soils: Tornquist et al. (2023) provide an update on soil carbon stocks in the Pampa region. They combine previously available and new datasets to build the most accurate map of soil carbon stocks possible at the moment and discuss the need to advance in this research topic, which is key to develop carbon-friendly strategies of land management and where grasslands – that hold high carbon stocks – may be an important element.

Part III, with two chapters, focuses on the forest–grassland interface. Bergamin et al. (2023) move away from the grassland and take a walk in the woods: they provide a synthesis on the forests that, albeit not dominant in the *Campos Sulinos* landscapes, form an important part of them. Based on a sample of ‘forests within the grasslands’, they found 675 tree species, with community composition influenced by both current and historical environmental drivers and species richness evidencing a clear decrease toward the South. Importantly, these forests have been heavily reduced in the past and are in need of conservation and restoration action. Müller et al. (2023) work at the forest–grassland interface: they describe the different expressions of the mosaics of both vegetation types that can be found in the *Campos Sulinos* region and their drivers. Grazing and fire, already pointed out as important factors in shaping grassland dynamics, are pointed out as key factors that determine forest–grassland boundaries. In the chapter, an integrative mechanistic model to explain forest–grassland dynamics is presented, the processes and traits of trees that facilitate establishment in open ecosystems are discussed.

While of course conservation as a topic permeates all chapters on biodiversity, it is the explicit focus of the Part IV of the book. Overbeck et al. (2023) provide a synthesis of the current conservation state of grasslands, with a focus on spatial aspects. They present updated information on the coverage by protected areas in the Campos Sulinos region, evidencing the very low protection level. Further, they discuss the potential contributions of Legal Reserves, but also the implementation gaps. Finally, they come back to the question of grassland management, a key topic for successful conservation of grasslands. Gallego et al. (2023) likewise focus on spatial analyses, but this time with a focus on the *Río de la Plata* region. They provide an overview of the primary land use and land cover changes that occurred in this region over the last two decades and discuss consequences for ecosystem functioning, the supply of ecosystem services, and the human appropriation of primary production. Finally, they evaluate the observed transition trends among land use and land cover and speculate on the most likely changes that may occur in the next few years. Beyond land use change, Guido et al. (2023) focus on one specific conservation problem: alien species invasions. Covering invasions by both exotic plants and animals, they start with a synthesis of key concepts of invasion biology that are of high relevance for any objective treatment of the topic. Different factors that drive or influence invasion processes are discussed, before moving on to management strategies and recommendations on how to deal with invasive alien species in the future. The section (and the book) closes with a chapter, by Thomas et al. (2023), on ecological restoration of the *Campos Sulinos* grasslands. The chapter gives an introduction to some key concepts of ecological restoration, a rather new topic for the *Campos Sulinos*, and presents the current state of art and research in the region: it becomes evident that both the practice of ecological restoration and the science of restoration ecology are still much at the beginning in southern Brazil, which makes it a challenge to meet international and national restoration goals.

1.5 The Future of the *Campos Sulinos*

The chapters in this book evidence the significant advancements in scientific knowledge on the *Campos Sulinos* over the past two decades, particularly regarding biodiversity and various conservation-related issues such as land use change, ecological restoration, and conservation strategies. However, there are still many gaps in our understanding. For many species groups, there is a lack of synthesis specifically for the *Campos Sulinos*, as is presented here for birds, mammals, and fish. Our knowledge on plant community composition in grasslands (Andrade et al. 2019) or forests (Bergamin et al. 2023, Chap. 15, this volume) is still based on small sample sizes, and for other types of ecosystems, there are no integrated studies encompassing the entire region. Further, there is a significant deficit regarding knowledge on ecosystem service provision in the *Campos Sulinos*. For instance, studies on the impact of land use change on hydrological cycles are scarce, as are studies on the relation between land management and pollination. Further, in the current debate on mitigating anthropogenic climate change, studies on how land use and land cover influence soil carbon stocks and carbon sequestration are highly relevant. Advances in these areas will be crucial for the conservation and sustainable development of the *Campos Sulinos*, especially considering livestock grazing, which is a type of land management that can contribute to the conservation of native grasslands while providing income for the local population. To achieve this, it is also necessary to conduct research that integrates social, economic, and environmental aspects, which is currently missing.

The future of the *Campos Sulinos* depends on halting the loss of grassland areas and implementing effective conservation methods. Global analyses on biodiversity and ecosystem services indicate that the natural resource base of our planet is deteriorating worldwide (IPBES 2019). The drivers of biodiversity loss and land degradation in the *Campos Sulinos* are similar to those in other regions of the world and include land use change, climate change, pollution, and invasive alien species. Scientific research has already provided consistent information on the necessary changes to conserve biodiversity and promote ecosystem services. However, what is lacking is a broader societal debate on these topics and the true integration of these issues into public policy. Despite the existence of legislation and political commitments, institutional capacity appears to be low, as evidenced by the limited coverage of protected areas in the region (Overbeck et al. 2023, Chap. 17, this volume). There are numerous pathways toward more sustainable management of *Campos Sulino*s landscapes, including payment for ecosystem services schemes, nature-based tourism, and the continuation and public support of extensive livestock-based grazing systems, among others. Indeed, this region, with extended native grasslands where many species are adapted to grazing, is one of the most suitable areas in the world for livestock production at low environmental impact. Political will is required to move in this direction, and to achieve this, a better valuation of the region's natural assets is necessary. It is our hope that the chapters in this book will convince readers of the immense natural capital in this region and of the need to preserve it for future generations, thereby contributing to the future of our planet. The conservation of the *Campos Sulinos* is also of global relevance.

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Part II

Setting the Scene: Origin, Environment, History of the *Campos Sulinos*

Chapter 2
Geological Memories of South Brazilian Landscapes: From Precambrian Orogenesis to the Quaternary Coastal Plain

Rualdo Menegat

2.1 Introduction

Southern Brazil, situated in the southeastern region of South America, is known for its stunning landscapes. Its features are formed by the vast sedimentary-volcanic Meridional Plateau superimposed on sedimentary rocks outcropping in its Peripheral Depression. Bordering this plateau at the East is the Atlantic Plateau, an extended band composed mostly by granites, migmatites, and gneisses (Vignol-Lelarge 1993; Hasui 2012c), which reach the coast as a prominent scarp, known as Serra do Mar. In turn, this coastal plateau is bordered here and there by fragmented coastal plains, with seaside lakes. To the West, the Meridional Plateau escarpment defines the sharp limit with the vast plain of the Chaco, in Argentina and Paraguay, already in a much more continental region of South America. Embedded in this large landscapes units, part of Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS) states, we find iconic scenarios of the natural history of South Brazil. At the western edge of the Meridional Plateau, for example, is one of the flashiest waterfalls on the planet, the Iguaçu Falls (from the Guarani language: *Y* = water; and *wai'su* = immense). Covering steep walls of volcanic rocks, water curtains with flow of more than 1.5 thousand liters per second, which may increase to 10 thousand per second in rainy seasons, collapse into the abyss in free fall, 82 meters downward (Fig. 2.1a).

The east and southern edges of the Meridional Plateau are outlined by a high escarpment whose elevation exceeds, at some points, 1700 m, cut out by sharp cracks, where dozens of magnificent canyons are located. The best-known and most impressive are, arguably, the canyons of *Itaimbezinho* and *Fortaleza dos Aparados*

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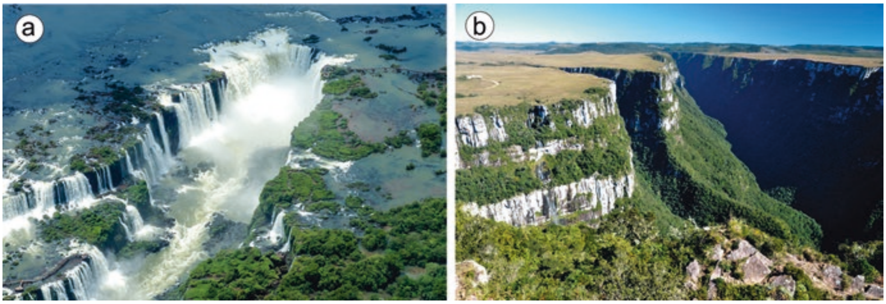

Fig. 2.1 (**a**) Aerial view of Devil's Gorge, Iguaçu Falls, Meridional Plateau's western edge (Photo by Enaldo Valadares, CC BY-SA 3.0). (**b**) Fortaleza Canyon, Meridional Plateau's east border (Photo by author)

da Serra (Fig. 2.1b). The dizzying faces of these abysses display successive volcanic flows that mark the first stages of the collapse of the former Gondwana supercontinent.

The basement of the thick volcanic-sedimentary package that constitutes the Meridional Plateau and its Peripheral Depression outcrops as a narrow coastal ribbon, known as Mantiqueira Province (Heilbron et al. 2004), parallel to the coast of the South Atlantic. Along the northern coast of the Mantiqueira Province, the magnificent Serra do Mar forms the geomorphological landscape of this basement, following the coastline (Fig. 2.2).

In its southern portion, the sedimentary and volcanic rocks of the Meridional Plateau form a tongue that reaches the coast and covers the basement, interrupting the Mantiqueira Province ribbon in a short segment. Here, the volcanic plateau escarpment substitutes the Serra do Mar and marks the coastline like a great curtain. The basement outcrops again at the very south but with much softer relief.

The high elevations in the northern portion of the Serra do Mar build the scenery for the flashy railway line from Curitiba, the capital of Paraná, to Paranaguá bay, on the coast (Fig. 2.3a). Farther away in the South, where the mountains find the sea, is another remarkable scenario of the southern region: the island that houses the capital of Santa Catarina state, Florianópolis (Fig. 2.3b). Its beaches, designed with sandy bays and granite points, are a destination for thousands of visitors in the summer and contain archaeological sites and petroglyphs of ancestral Amerindian cultures.

Further south, in the state of Rio Grande do Sul, the Precambrian basement is more eroded and wider than the ribbon to the north. Denominated as the Sul-Rio-Grandense Shield or Plateau, it widens toward the West, where it finally reaches the elevation of the Peripheral Depression lowlands. Along the eastern flank of this basement, we find one of the world's longest coastal plains, with a total length of 620 km (Dillenburg et al. 2009). Dozens of small lakes and several huge lagoons are distributed within this plain, including Laguna dos Patos and Lago Guaíba. Porto Alegre, the capital of Brazil's southernmost state, Rio Grande do Sul, is located on the northeastern shore of the latter (Fig. 2.3c).

Fig. 2.2 Relief shading map of southern Brazil and adjacent regions. The locations shown on the map in yellow and white are referred to in the text. (Source: image licensed from © Anton Balazh, 123RF.COM; NASA digital model data; cartography by author)

Great geodiversity and biodiversity make up these large landscape settings, including the vast grasslands that extend from the southern lowlands to the high altitudes of the North. This chapter will discuss the geological memory and evolution of these lands that are a hallmark of South America. The crucial questions here explored are how the ancient supercontinent Gondwana was structured by colliding microcontinents and how it fragmented into present-day South America. The main geotectonic events that structured the Precambrian Mantiqueira Province, the basement of the Paraná Basin, will be considered in detail. The central sedimentary units that contain an excellent fossil collection of this basin will be described. Further, we will investigate the massive Cretaceous volcanism that marks the beginning of the fragmentation of Gondwana. This geological evolution ends with the Quaternary processes that formed the Atlantic coastal plain as South America continues its long geological journey westward.

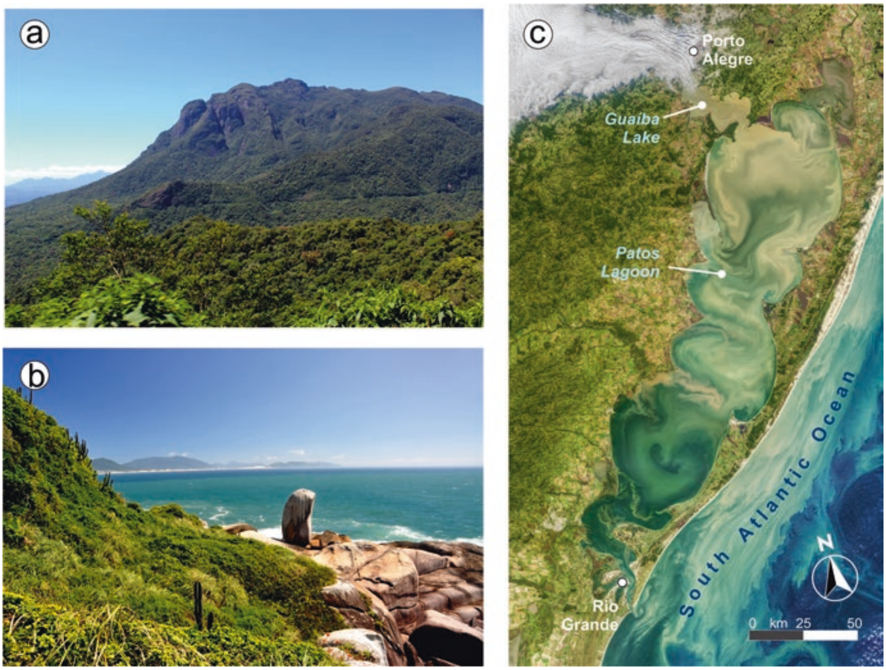

Fig. 2.3 (**a**) Curitiba-Paranaguá Railway line crossing mountains of the *Serra do Mar*. [Photo by Saturnalia, CC BY-SA 3.0] (**b**) Florianópolis' granitic coast, southern *Serra do Mar*. (**c**) Landsat image of the *Patos* Lagoon, suspended sediment, phytoplankton, submerged aquatic vegetation, and colored dissolved organic matter highlight the vortices flux. (Photos by author; Landsat Image by NASA/OBPG/OB.DACC (2018) and cartography by author)

2.2 The Tremendous Geological Provinces: Records of Remnant and Recent Continents

Three great compartments of a long geological memory that extends from the Archean to the Quaternary period constitute the crustal basement of southern Brazil. From oldest to youngest, these central geological provinces (Fig. 2.4) are (a) the Mantiqueira Province, structured by ancient rocks from the Archean to Proterozoic Eons, which coincides with the Atlantic Plateau, a geomorphological unit; (b) the Paraná Province, constituted by a thick sedimentary-volcanic package formed from the Silurian (Paleozoic) to the Cretaceous (Mesozoic), whose highlands coincide with the Meridional Plateau and the lowlands match with its Peripheral Depression; and finally, (c) the Coastal Plain, which consists of sandy and muddy deposits from the Quaternary period (Schobbenhaus and Neves 2003). The lithological patterns and the stratigraphic way they succeed each other, associated with the geotectonic structures of these compartments, form a unique geomorphology that can be seen as a kind of landscape DNA of this vast region in South America.

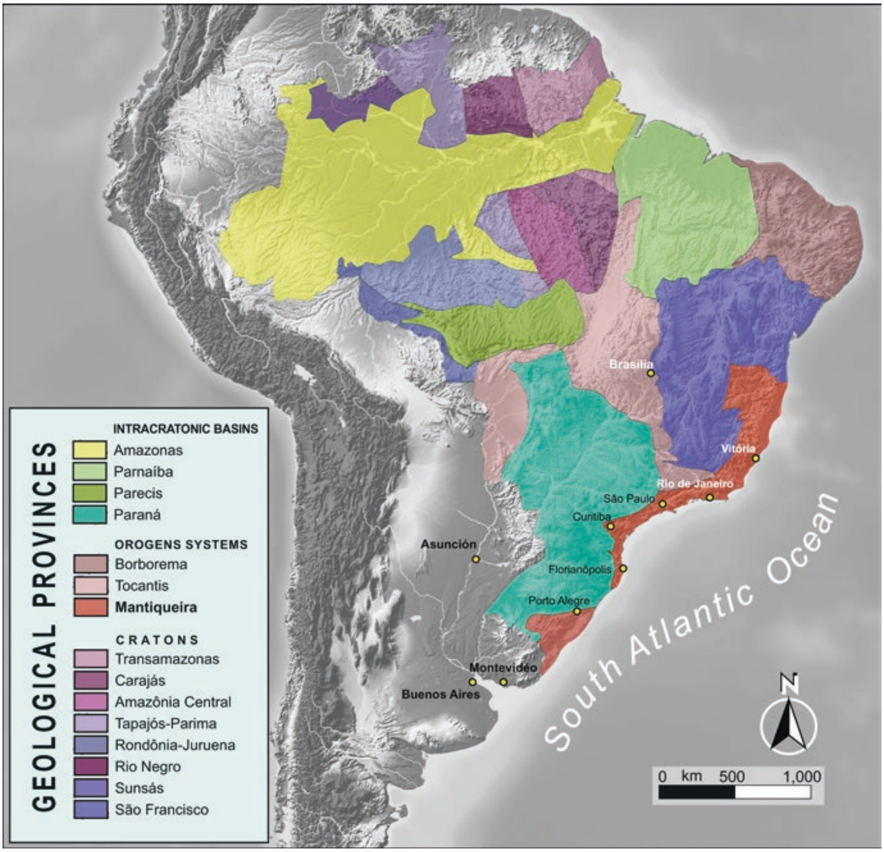

Fig. 2.4 Map of the Brazilian Geological Provinces. (Data from Delgado et al. 2003; cartography by the author)

2.3 The Mantiqueira Province: The Orogenesis that Structured a Supercontinent in the Precambrian

The magnificent landscapes of Brazil's southern coast, which include the Serra do Mar mountain range and the majestic geomorphological formations such as the Sugarloaf Mountain in Rio de Janeiro, result from tectonic faults and the erosion of granitic and gneisses rocks of the Mantiqueira Province (from Tupi Language, amantikir = 'the mountains that cry,' in reference to the many river springs). It is a narrow coastal plateau about 200 km wide, forming a coastline drawn by rocky points and inlets carved by the sea, sometimes with small sandy plains with lagoons. To the South, the high mountains of the north give way to the remnant plateau (maximum of 500 m high) of the Sul-Rio-Grandense Shield.

Most of the Mantiqueira Province is composed of igneous intrusive and high- to medium-grade metamorphic rocks, with small occurrences of siliciclastic rocks

(Delgado et al. 2003; Heilbron et al. 2004; Hasui 2012c) (see the main rock type in Table 2.1). The rocky units are grouped into three large domains, also arranged as narrow northeast-oriented bands, which geologists call Brasiliano I, II, and III Orogen Systems (see Fig. 2.5). These orogen systems include small areas composed of Archean rocks that represent fragments of ancient continents, known as cratons, or microcontinents. An orogen is the term that geologists use to represent a broad-scale geotectonic event, leading to the formation of mountain ranges during an orogenesis. Orogens often include multiple mountain belts, basins, and other associated features and their typical rock assemblages (Sengör 1990). The word 'craton' refers to an old, stable portion of the continental lithosphere in relation to another that was tectonically active during orogeny (Alkmim 2004).

The three orogen systems keep records from the long history of several diachronic orogenic processes structured by the closure of oceans and collisions of small continents, today represented by the cratons. This process, which goes from 880 to 520 Ma (from Mega annum = million years), constituted the Western Gondwana Supercontinent in the Neoproterozoic and early Paleozoic (Silva et al. 2005). To understand this better, we will first locate the prominent cratonic nuclei that represent the continents that collided and formed the supercontinent during this period.

We start in the southern end of the Mantiqueira Province, at the western edge of the Sul-Rio-Grandense Shield, where a small portion of the Rio de La Plata Craton outcrops (Babinski et al. 1996; Leite et al. 1998). Evidence indicates that this craton extends southward under the thick sedimentary and volcanic package of the Paraná Basin, outcropping again in Uruguay and Argentina and northward as the basement of the Paraná Basin (Rapela et al. 2007; Gaucher et al. 2008). Geologists assume that the granulites (high-grade metamorphic rocks) of this craton originated in an ancient island arc of about 2.5 Ga (Giga annum = billion years) at the boundary of the Neoarchean and Paleoproterozoic Era (Hartmann et al. 2001; Hartmann and Delgado 2001). Further north, in Santa Catarina, the Luís Alves Craton outcrops, composed of granulite around 2.7 Ga (Hartmann et al. 2000), considered by many authors as part of the Rio de La Plata Craton (see Hasui 2012a).

The interaction of several convergent plates formed many orogens over time, constituting a system of orogens, such as the Mantiqueira Province (Delgado et al. 2003, Heilbron et al. 2004). Thus, this province records an orogenic collage of orogen systems that led to the formation of the Gondwana Supercontinent (Neves et al. 1999; Basei et al. 2008). The main cratons amalgamated by collisions were Rio de La Plata (and Luís Alves and other microplates), the São Francisco and the Amazon in Brazil, and the Kalahari and the Congo cratons in Africa. The Kalahari Craton (Clifford 1970; Jacobs et al. 2008) today is part of South Africa, Botswana, Namibia and Zimbabwe, and the Congo Craton (Schlüter 2008) is in southwestern Africa. The São Francisco Craton (Dominguez and Misi 1993; Alkmim 2004) is considered a counterpart of the Congo Craton (see Fig. 2.6) These collisions generated the Brasiliano-Panafrican orogeny structured in several phases and orogens (Neves et al. 1999; Delgado et al. 2003; Silva et al. 2005; Hasui 2012c).

Table 2.1 The Brasiliano Orogens Systems and main rock types by orogen[a]

Orogens System (Numerical age in Ma)	Orogen[b]	Tectonic context	Main rock types
Brasiliano III *590 to 520*	*Búzios* Adamastor Ocean closure	Continent-continent tectonic plate convergence	*[No occurrence in Brazil's southern states RS, SC, PR]*[c] Gneisses, migmatites, granitoids
	Araçuaí-Rio Doce Continental collision of the Amazon + São Francisco Cratons with the Congo Craton Adamastor Ocean closure	Synorogenic magmatic arc	*[No occurrence in Brazil's southern states RS, SC, PR]*[c] S- C-type syncollisional granites and gneisses, granites to tonalites, migmatites, S-type leucogranites, charnockites, enderbites, norites and gabronorites, volcanic-sedimentary rocks
Brasiliano II *640 to 610*	*Rio Negro* Adamastor Ocean closure	Continental magmatic arc	*[No occurrence in Brazil's southern states RS, SC, PR]*[c] Metavolcanic-sedimentary rocks, orthogneisses, banded gneisses, granulites rocks, calc–silicate rocks, mica schists, quartzites, metamaphytes, limestones, syn- to post-tectonic granitoid, charnockites
	Embu Allochthonous terrain	Context unknown	Paragnaisses, tonalitic to granodioritic orthogneisses, mica schists, quartzites, calc–silicate rocks, amphibolites, metaultramaphytes
	Paranapiacaba Collision of the S. Francisco-Congo + Luis Alves + Rio de La Plata cratons with the Curitiba microplate // Adamastor Ocean closure	Castro basin Continental rift	Volcanic-sedimentary rocks: ignimbrites, volcaniclastics, rhyolites, quartz-latites, andesites, conglomerates, arkose sandstones, siltstones, mudstones
		Continental magmatic arc	Granitoids and retro-arc volcanism Ophiolite’s metabasaltic remnants

(continued)

Table 2.1 (continued)

Orogens System (Numerical age in Ma)	Orogen[b]	Tectonic context		Main rock types
	Pelotas Collision of the Kalahari Craton with the Rio de La Plata craton + Luis Alves microplate; Adamastor Ocean closure	Foreland basins	Camaquã and Itajaí	Volcanic-sedimentary rocks: bimodal affinity volcanic rocks, rhyolites, trachytes, dacites, basalts, ignimbrites, conglomerates, sandstones, arkoses, mudstone, siltstone, shales, turbidites
			Campo Alegre	Felsic volcanic rocks, ignimbrites, volcaniclastics, basalts, andesites, trachytes, conglomeratic sandstones, siltstones, turbidites, mudstones
			Guaratubinha	Andesites, rhyolites, volcaniclastics, ignimbrites, conglomerates
		Post-tectonic intrusions		Subalkaline granites (A-type) and alkaline and shoshonitic varieties
		Pelotas, Florianópolis, Paranaguá Batoliths		High-K alkaline granitic rocks, S-I-A-types granitoids, charnockites, monzogranites, syenogranites, leucogranites Tonalitic gneissic remnants
Brasiliano I *880 to 700*	*São Gabriel* Collision of the volcanic arc with the Rio de La Plata Craton; Charrua Sea closure	Intraoceanic arc-rock assemblages and ophiolitic associations		Quartzites, schists, phyllites, graphite schists, metalimestones, metacherts, metamaphytes and metaultramaphytes, pillow mafic lavas, slates, metaconglomerates, and metabasalts
Cratons and inliers *2.700 to 2.500*	*Micro-continents*	Rio de La Plata Craton (2.55 Ga)		Orthogneisses, TTG granulites with maphyte – ultramaphytes enclaves, paragneisses, mica schists, quartzites, calc–silicate rocks
		Luís Alves (2.6 Ga)		Maphytes and ultramaphytes, granulitic, dioritic, monzodioritic, monzonitic, syenitic, granodioritic, tonalitic and leucogranitic granulites; kinzigites, granulitic pyroxenites, quartzites.
	Single fragments	Encantadas (RS), Camboriú (SC), Curitiba (PR)		TTG orthogneiss, amphibolite, tonalite, leucogranite, metaandesite

[a] Data from Fernandes et al. (1995a), Hartmann et al. (2001), Heilbron et al. (2004), Silva et al. (2002), Delgado et al. (2003), Teixeira et al. (2004), Hasui (2012c)

[b] See Fig. 2.6, Map of the Brasiliano Orogens Systems, for unit location

[c] No occurrence in the three southern states of Brazil: *RS* - Rio Grande do Sul, *SC* - Santa Catarina, *PR* - Paraná

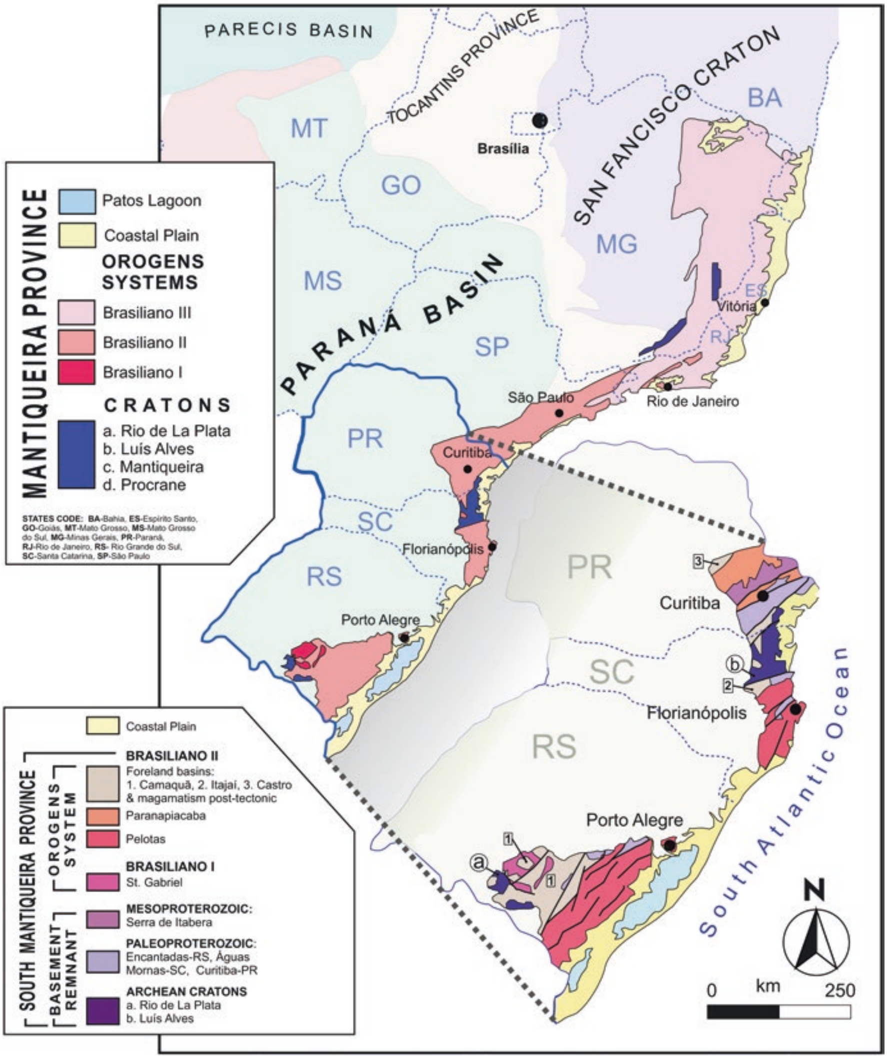

Fig. 2.5 Map of the Mantiqueira Province's Orogen Systems and mayor cratons (top), and detailed Map of the South Brazilian Region (bottom, enlarged). (Data from Delgado et al. 2003; cartography by author)

The first phase of these ancient plate collisions corresponds to the Brasiliano System I, which is exposed in a small area of 5000 km^2 very close to the Rio de La Plata Craton, in the west of the Sul-Rio-Grandense Shield (Delgado et al. 2003; Hartmann et al. 2011). This system developed predominantly between 880 and 700 Ma (Tonian and Cryogenian Periods, Neoproterozoic Era), and consists of a single orogen named São Gabriel. Its rocks were formed in an intraoceanic volcanic

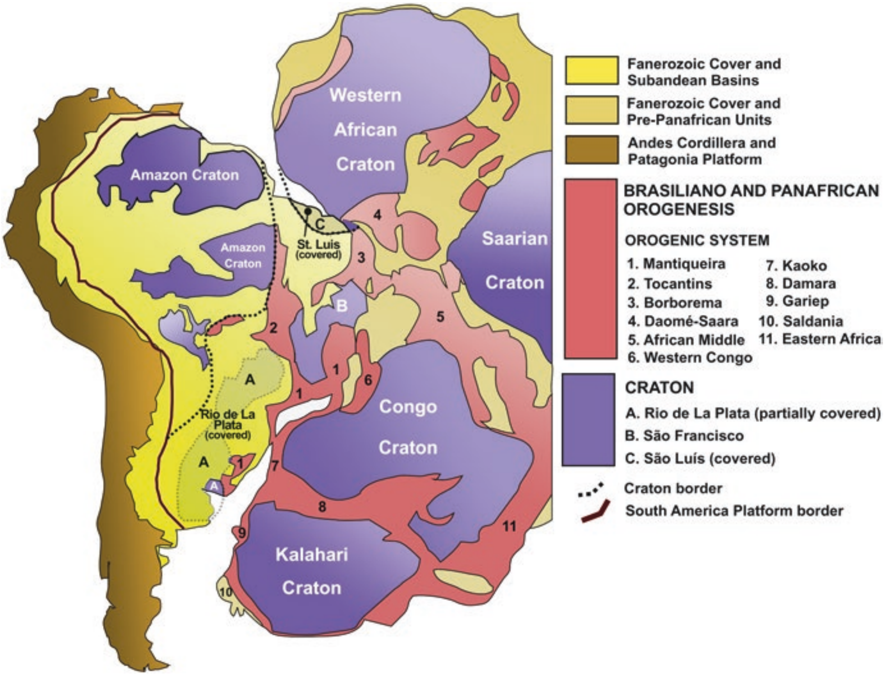

Fig. 2.6 Cratons and Mantiqueira Province location in the Brasiliano-Panafrican orogenesis. (Data from Linol and Wit 2018; cartography by author)

arc that collided with the Rio de La Plata Craton, leading to the closure of an ancient Charrrua Ocean (see Fig. 2.7). In the São Gabriel Orogen, records of an ophiolite are interpreted as remnants of the Charrua Ocean floor (Fernandes et al. 1995a, b; Babinski et al. 1996; Leite et al. 1998; Menegat et al. 2006a).

The second phase of the orogenesis, represented by the Brasiliano Orogen System II, established between 640 and 610 Ma (Cryogenian and Ediacaran Periods of the Neoproterozoic Era). It comprises three collisional orogens, namely Pelotas (in Rio Grande do Sul and Santa Catarina), Paranapiacaba-Rio Pen (in Paraná and São Paulo), and Rio Negro (in São Paulo and Rio de Janeiro), as well as the Embu terrain. With a longitudinal extent of more than 1000 km, this system consists of large intrusive batholiths generated during the collision. Included here are the batholiths known as Pelotas (in Rio Grande do Sul), Florianópolis (in Santa Catarina), and Paranaguá (in Paraná), of the Pelotas Orogen, which are composed of high-K calc-alkaline granitic rocks (Silva et al. 2002; Delgado et al. 2003).

The Brasiliano Orogen System III represents the third phase. It occurs only in the very northern portion of the Mantiqueira Province and was structured in the late Ediacaran Period (Neoproterozoic Era) and early Cambrian Period (Paleozoic Era), between 590 and 520 Ma (Silva et al. 2002).

The Supercontinent Gondwana was already structured at the beginning of the Paleozoic Era (Rapela et al. 2007; Hasui 2012c). In its western portion, the collision

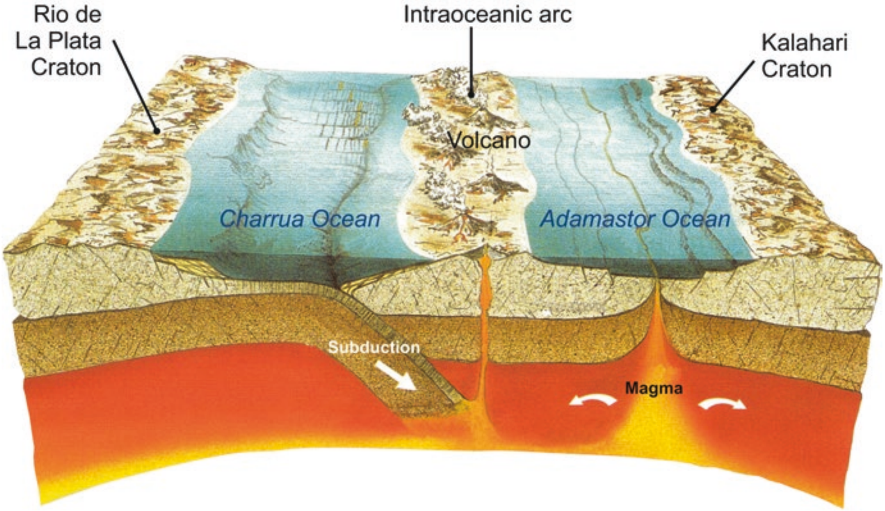

Fig. 2.7 The Brasiliano Orogen I recorded the closure of the Charrua Sea by the collision of the intraoceanic arc (middle) and the Rio de La Plata craton (left), with subduction from the west ocean plate. (Modified after Menegat et al. (2006a); by courtesy of Atlas Ambiental de Porto Alegre, 2006)

of several microcontinents – Rio de La Plata, Luís Alves, São Francisco and Amazon in South America, and Kalahari, Congo and West Africa in Africa – gave rise to an extensive mountain range, similar to the Himalayan Mountains. Part of the so-called Brasiliano-Panafrican belt (see Fig. 2.6) is recorded in Brazil by the Mantiqueira Province, which is at the eastern border of the Rio de La Plata, Luís Alves, Curitiba, San Francisco, and Amazon cratonic nuclei (Neves et al. 1999).

A mountain range does not evolve without sedimentary basins associated with it. Geologists call these ‘foreland basins’ or ‘strike-slip basins’, among other terms. By investigating the base of the sedimentary sequence that filled it, researchers may find the mountaintop rocks of the Brasiliano-Panafricano belt that eroded in the early stages. Associated with Brasiliano Orogens, there are many remnants of these basins (Guadagnin et al. 2010; Basei et al. 2011). The most significant is the so-called Camaquã Basin in Rio Grande do Sul, which comprises a 7000-m-thick sedimentary and volcanic sequence (Menegat and Fernandes 2001a, b, 2003, Teixeira et al. 2004). However, the sequence is no longer at the *locus* of its depositional origin. It outcrops as tilted fragments and the exploration of its complete evolution constitutes a puzzle for geologists.

After the end of the significant continental collision phase, a period of crustal relaxation established, causing the depression of the surface regions, and forming a new phase of extensive sedimentary basins, identified as intracratonic basins, such as the Paraná Basin. The source of sediments in these basins included the Brasiliano Range (Carneiro et al. 2004).

2.4 Paraná Province: A Complete History of the Western Gondwana Supercontinent in Paleozoic and Mesozoic Eras

The installation of the Paraná Basin and its counterparts in Africa, the Karoo and Kalahari basins, occurred in the southwestern portion of Gondwana Supercontinent. In the Paraná Basin, no less than 7500 m of sediments and volcanic lavas accumulated over 400 million years. It forms a remarkable record of the evolution of the supercontinent, from its tectonic stabilization in the Late Ordovician (Paleozoic Era), to its complete fragmentation in the Late Cretaceous, the occlusion of the Mesozoic and the dawn of the Cenozoic Era (Greek for recent life). The Paraná Basin occupies about 1,700,000 km^2, of which 1,100,000 km^2 are in Brazil, including the three southern states (RS, SC, and PR), as well as São Paulo, Mato Grosso do Sul, Mato Grosso, Goiás, and Minas Gerais. The remaining 600,000 km^2 are in eastern Paraguay and Argentina, and western Uruguay (Milani 1997, 2007; Milani et al. 1998, 2007; Milani and Zalán 1999; Zalán 2004).

The thick volcano-sedimentary sequence can be divided into six second-order allostratigraphic supersequences, limited at the base and top by extensive unconformity surfaces (see Figs. 2.8 and 2.9). The supersequences are known by the following names from base to top (in parentheses are the Epoch or Age, followed by Period of the base and top boundaries, respectively): Rio Ivaí (Upper Ordovician-Llandovery, Silurian), Paraná (Lockovian-Frasnian, Silurian), Gondwana I (Middle Pennsylvanian, Carboniferous-Early Triassic), Gondwana II (Anisian-Norian, Triassic), Gondwana III (Upper Jurassic-Berriasian, Cretaceous) and, at the very top, Bauru (Aptian-Maastrichtian, Cretaceous). Each supersequence encompasses lithostratigraphic formations, described below with their respective lithologies and paleo-environments (Milani 1997, 2004).

The deposition of the two basal supersequences, Rio Ivaí and Paraná, was produced in the Late Ordovician-Silurian and Devonian, respectively (Mizusaki et al. 2002; Quadros 2007). In Southern Brazil, they are exhibited not only in eastern Paraná, near the Curitiba region, but also in the northern part of the Paraná Basin, in Mato Grosso, Goiás, and Mato Grosso do Sul. The most significant thickness, located in Paraguay, reaches 1000 m. A common lithologic succession of the Rio Ivaí Supersequence includes, at the base, a 300-m package of conglomerates and sandstones of the Alto Garças Formation and diamictites of the Iapó Formation. The rocks of Iapó highlight the occurrence of the Late Ordovician-Early Silurian glaciation in Gondwana. On the top, micaceous shale and fine sandstone of the Vila Maria Formation are identified, containing faunas of chitinozoan and graptolites (Grahn et al. 2000).

The regressive-transgressive marine package of the Rio Ivaí underlies the Paraná Supersequence (Pereira et al., 2007). At the base, this supersequence includes coarse-grained, kaolinite-rich sandstones of the Furnas Formation overlain by deltaic sandstones and marine shales of the Ponta Grossa Formation. This unit contains a great diversity of invertebrate fossils, such as Conulariida, Brachiopoda, Ostracoda,

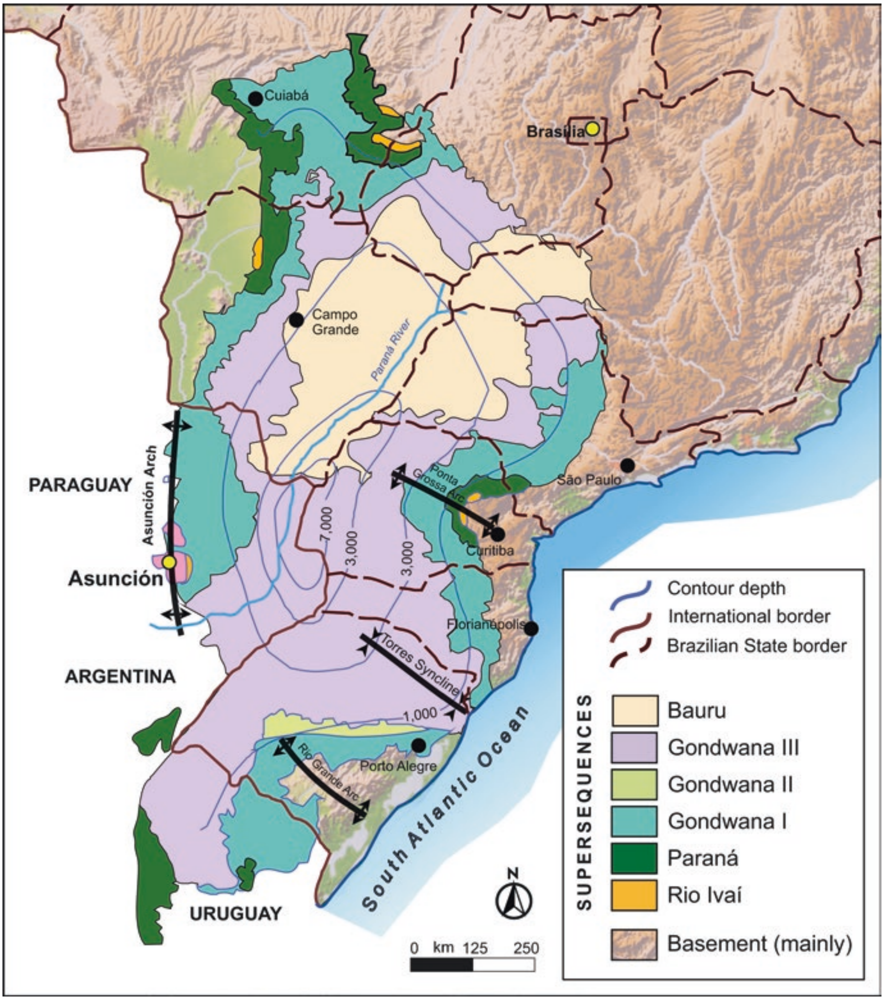

Fig. 2.8 Map of the supersequences and isopaques of the Paraná Basin. (Data from Milani 2004; Cartography by author)

Bivalvia, Gastropoda, Tentaculitoidea, Trilobita, and Crinoidea, as well as ichnofossils of the Zoophycus ichnofacies, and plant remains, such as Spongyophyton (Quadros 2007; see Fig. 2.9).

A long gap of 55 Ma marks the boundary between the Paraná package and the Gondwana I Supersequence. This long lag is due to the installation of an Antarctic-type ice sheet related to Carboniferous-Permian glaciations when the southern region of the Paraná Basin was very close to the South Pole (Castro 2004; Wit et al. 2007). With a maximum thickness of 2500 m, this supersequence is the largest in the basin. It has maintained a complete record of the Late Carboniferous to Late Permian interval of the supercontinent Gondwana. There is also significant fossil content of plants

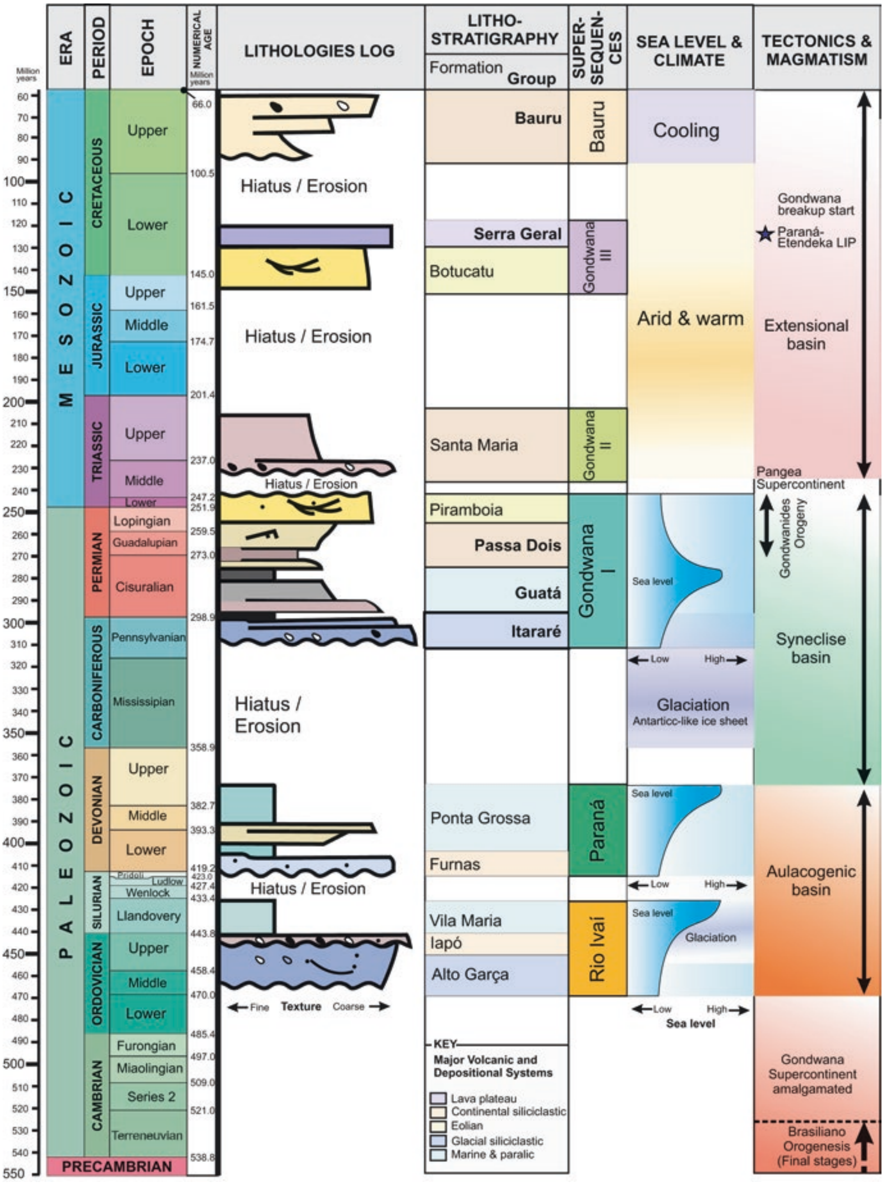

Fig. 2.9 Simplified Stratigraphical column of the Paraná Basin and main sea level changes and tectonic/magmatic events. (Data from Milani et al. (2007), Carneiro et al. (2004), Cohen et al. (2023))

such as *Glossopteris*, *Noeggerathiopsis*, *Sphenophyllum*, *Gangamopteris*, *Arberia*, *Asterotheca*, *Phyllotheca*, *Botrychiopsis*, *Nothorhacopteris*, and *Paranoclodus* (Rösler 1978; Rohn 1997; Iannuzzi 2000); invertebrates such as *Pinzonella*, *Australomya*, *Jacquesia*, *Heteropecten*; and *Schizodus*, and palynomorphs as *Potonieisporites*, *Lundbladispora*, *Vittatina*, *Weylandites*, and *Cannanoropollis* (Quadros 2007).

At the base, the Gondwana I supersequence records a 1500 m-thick package resulting from the disappearance of glaciation that extended from the Carboniferous (Moscovian Age) to the Permian (Sakmarian Age) Periods. In the basal deglaciation record, diamictites interfingering with sandstones of the Itararé Group are found in the south and correlated to the Aquidauana Formation in the north of the basin. The mild climate enabled the development of forests formed by glossopterids, lycophytes, and peat bogs formed the coalfields of southern Brazil (Cazzulo-Klepzig et al. 2005; Jasper et al. 2006; Guerra-Sommer et al. 2008). These forests were established in lowland environments in the estuaries and deltas of the coastal zones of an epicontinental sea, as evidenced by the siltstones, sandstones, and carbonaceous shales of the Rio Bonito Formation (see Fig. 2.10). An extensive marine transgression drowned the coastal environments and was marked by the shales and fine sandstones of the Palermo Formation. The onset of regression was recorded by siltstones, gray claystones, and organic-rich claystones interfingered with limestones of the Irati Formation (Upper Permian). This unit is well known for the diversity of its fossil content, which includes plant megafossils (Rohn and Rösler 2000), vertebrates, invertebrates (insects, crustaceans, and foraminifera), palynomorphs (as pollen grains and spores) and ichnofossils (Mussa et al. 1980; Oelofsen and Araújo 1983; Pinto and Adami-Rodrigues 1996). Among vertebrates, mesosaurs (Progranosauria, genera *Mesosaurus*, *Stereosternum*, and *Brazilosaurus*) are commonly used for correlation with the Karoo Basin in Africa. Furthermore, the Irati Formation is the most critical unit in the basin in terms of oil generation (Santos et al. 2006).

This glacial-transgressive package, whose formations are collectively included in the Guatá Group, was overlain by the 1400-m-thick regressive packages represented by the Passa Dois Group (Rohn 2007). The top of the Gondwana I Supersequence is marked by aeolian sandstones of the Sanga do Cabral and Piramboia formations, deposited in the Early Triassic, representing the continuing vanishing of basin's sea environments and the increasing installation of a warm and arid climate (Assine et al. 2004). These rocks mark an essential change in the geomorphological, climatic, and environmental conditions of the basin. They recorded the end of a long period of icehouse climate and the beginning of a long period of greenhouse climate.

The Gondwana I Supersequence recorded not only changes in climatic conditions but also changes in basin-forming mechanisms. During the deposition of this transgressive-regressive package, the working mechanisms were those of a syneclise resulting from intracratonic stability in the Paraná Basin invigorating during the Silurian to Permian (Carneiro et al. 2004). In the Permian Period, a magmatic arc named Choiyoi (Japas and Kleiman 2004), associated with the Gondwanides

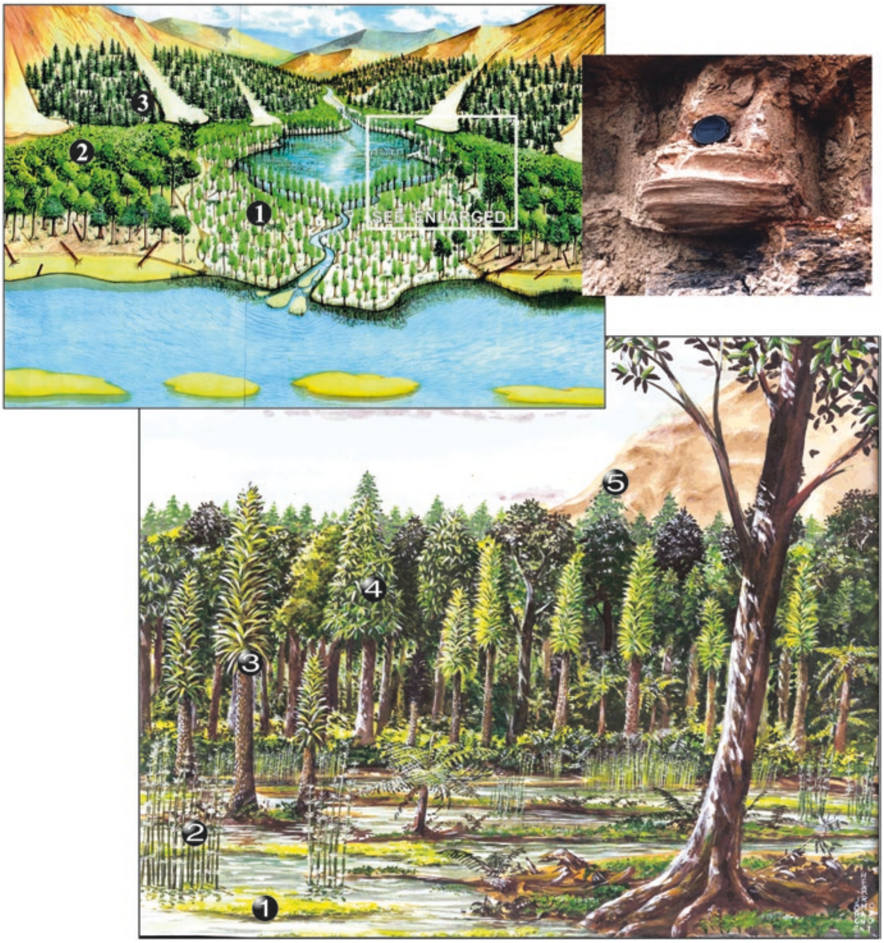

Fig. 2.10 Clastic swamp landscape unit plant communities (Southern Paraná Basin). Upper left: a general view of paleo-environments: (1) Lycophyta community on clastic swamp, (2) *Glossopteris* community on drained lowland, (3) Conifer community on distal alluvial fan. In the enlarged drawing, plant community detailed are: (1) Lagoon: algae and *incertae sedis*; (2) Lagoon margin: Filicophyta, Sphenophyta, and herbaceous Lycophyta; (3) Humid lowland: arbustive and arborescent Lycophyta; (4) Drained lowland: Glossopteridophyta and Cordaitophyta; (5) Drained lowland to highland: Coniferophyta. Inset photo, Licophyta trunk base fossil in Quiteria outcrop (After Cazzulo-Klepzig et al. 2005; photo by author)

orogenesis, settled on the southwestern margin of the supercontinent, closing the communication of this intracontinental basin with the Pantahalassa Paleocean (a proto-Pacific), providing the deposition of the regressive event of the Passa Dois Group (Milani 2007). However, a significant phase of tectonic activation by extensional faulting occurred from the Middle Triassic onward. With the end of the compressive forces acting on the magmatic arc since the Permian, there was a wide extension and collapse of crustal blocks, such as grabens (term used to designate a block of land with escarpments on both sides than moved downward), in the southern basin. The lacustrine deposits that filled these grabens are nowadays exposed only at the southern end of the basin, in the Peripheral Depression of the Rio Grande do Sul. These deposits comprise the Gondwana II Supersequence, overlying Gondwana I, composed of conglomerates and sandstone from dense currents that flew into lakes (Borsa et al. 2017; Lima et al. 2018). This red-bedded package, known as the Santa Maria Formation, contains vertebrate fossils that represent a crucial Triassic fauna of ancestral dinosaur and mammal species. The primary vertebrates include tetrapods (*Thrinaxodon*, *Chiniquodon*, *Rhynchosauria*, *Dinodontosaurus*, *Prestosuchus*, and *Hyperodapedon*) (Kellner and Campos 2012; Soares et al. 2012; Francischini et al. 2015). In addition, this epoch coincides with the collision of the supercontinents Gondwana and Laurasia, located further north, forming the supercontinent Pangea.

The penultimate supersequence formed in the supercontinent, known as Gondwana III, is very different from the previous ones and marks a new tectonic, paleogeographic and climatic condition: the beginning of the collapse of Gondwana and Pangea when the present continents individualized. At the base of this sequence, overlying the Triassic rocks of the Gondwana Supersequence II, is about 400-m-thick Botucatu Formation. It consists of medium to fine sandstones with large cross-bedding originating from dune fields of a regionally widespread desert prevailed in the Late Jurassic (Assine et al. 2004).

Finally, overlying the Botucatu sandstone is the 1700-m-thick package of bimodal basic–acid composition (basalt and dacites to rhyolite) of the Lower Cretaceous Serra Geral Group (Wildner et al. 2007; Mizusaki and Thomas-Filho 2004; Rossetti et al. 2018). These rocks are distributed over 1.2 million km^2 and constitute the top of the Paraná Basin in southern Brazil, except in the northwestern Paraná. The composition of tholeiitic basalt (with two pyroxenes, augite and pigeonite) is distinguished into high-Ti and low-Ti. High-Ti basalts occur in the north of the basin, while low-Ti basalts and rhyolites are distributed in the center and southeast (Melfi et al. 1988; Marques and Ernesto 2004; Gomes et al. 2018). Along the stratigraphic profile, compositional flow types are interfingered so that the composition is not sufficient criteria for lateral correlation.

Furthermore, the base of the Serra Geral Group comprises sandstone beds interfingering with a volcanic flow. It is noticeable that the first lava flow extruded over the active dunes, preserving the geomorphology of the erg's depositional surface (Waichel et al. 2008). However, sandstones of the interfingered package show structures and facies of streams, providing support for interpreting different climatic conditions during the interval of the lava flows from those invigorating during the deposition of the Botucatu aeolian sandstone, which occurred in an arid context (see Fig. 2.11). Many stratigraphic levels contain evidence that lavas interacted intensely with water-saturated sand and groundwater, generating features typical of explosive interaction between water and magmatic processes (Petry et al. 2007; Rios et al. 2018; Licht and Arioli 2020).

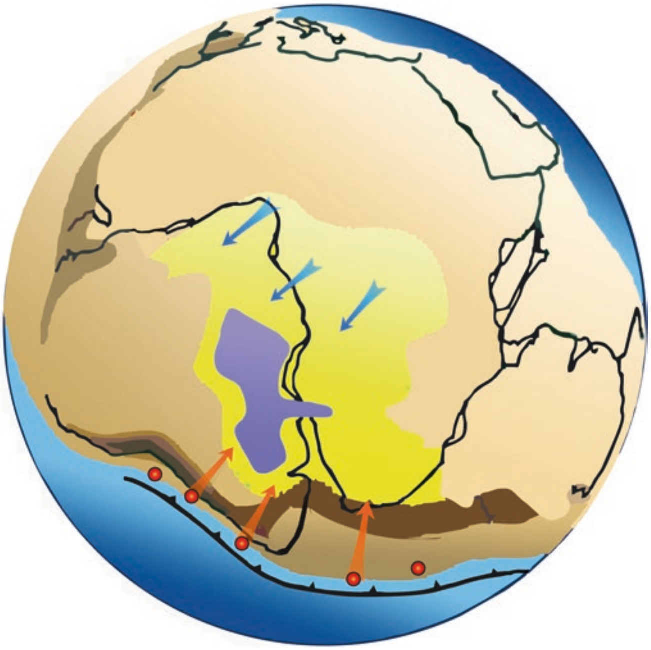

Fig. 2.11 Botucatu Desert (estimated area in yellow) and Paraná-Etendeka Large Igneous Province (purple) in Western Gondwana, Lower Cretaceous. Red arrows indicate volcanic plumas flowing northeasternward from the volcanic arc in a convergent plate context between the Panthalassa seafloor and the western Gondwana border. Blue arrows mark the southwestern palaeowind currents. (Data from Linol and Wit 2018; cartography by author)

This group of tholeiitic volcanic rocks, primarily basalts, and basaltic andesites, marks the earliest of the fragmentation of the supercontinent Gondwana. Paraná-Etendeka Large Igneous Province, as this magmatism is known, is one of the largest in the history of the planet (Guimarães et al. 2018; Licht and Arioli 2020). Most of the flows occurred over an interval of only 1.2 million years, with the climax around 134 Ma (Licht and Arioli 2020). The complete separation of South America and Africa occurred 66 million years ago, since then South America has drifted westward until today, when it reaches a rate of 3.5 cm/year.

In the Late Cretaceous, under extensional tectonic conditions in the north of the basin, alluvial, fluvial gravel, and aeolian sand sedimentation occurred, constituting the Bauru Supersequence. This sequence overlaps volcanic rocks only in the northwest of the Paraná State and extends to the northern edge of the basin. Some units include Senonian fossils represented by Chelonia, Crocodilia, and Dinosauria (Quadros 2007).

2.5 The Gondwana Fragmentation and the Rising of the Meridional Plateau and the Serra do Mar in the Cenozoic Era

The fragmentation process of the supercontinent Gondwana started in the Late Jurassic. In the current southeastern and southern Brazilian coast, an extensional regime was installed, leading to the formation of normal faults with the sinking of crustal blocks, called rift valleys by geologists, as in the Great East Valley of Africa (Schobbenhaus and Neves 2003; Hasui 2012b; Riccomini et al. 2004; Mohriak 2004). Every crustal fragmentation process begins with crustal uplift due to a thermal anomaly from a mantellic hop spot, with crustal rifting and the formation of a triple junction with three rifts diverging from one point. With continued extensive stresses, the crust separates along two rifts, which become the margins of the new continents, and the third rift is abandoned (Hasui 2012b). Along the southeastern coast of Brazil, the Serra do Mar shows two trends (see Fig. 2.12). One is the E-NE direction in the region of São Paulo and Rio de Janeiro, and other is the N-NE direction from southern Paraná to Santa Catarina. These two directions identify the two arms of the former triple junction where the crust broke up. For this reason, the coast in this region assumes an elbow shape with the open angle pointing to the southeast, forming a sea inlet, as in an open bay. The NW-oriented swarm of mafic dikes, the Ponta Grossa Arc, marks the abandoned third rift.

These processes resulted from the opening of the South Atlantic Ocean, which occurred from South to North. The climax of rifting took place in the Early Cretaceous, with the extrusion of basaltic lavas of the Serra Geral Group in Brazil and the Etendeka in Africa, with climax at 134 Ma (Thiede and Vasconcelos 2010). The emergence of the oceanic crust and the center of expansion of the South Atlantic floor between the two continents occurred between the Aptian and Albiano Ages (121 to 100 Ma). The scars of this continental collapse are visible not only in the volcanic flows of over 900 km^3 of lava that generated the Paraná Large Igneous Province. The events that followed the burial of the Botucatu desert by a basaltic lava desert during a significant time interval led to the formation of prominent geomorphological features on the Brazilian coast, indeed through the Paleogene.

Along the southeastern coast of Brazil, a succession of elongate east-northeast grabens, known as the Southeast Continental Rift System, formed, extending from Espírito Santo, Rio de Janeiro and São Paulo to the northern Santa Catarina state. These rifts formed a series of high and low blocks on the east edge of the Atlantic plateau, constituting a sizeable coastal escarpment with narrow beach plains. The erosion of the cliffs and the high blocks resulted in the carving of the Serra da Mantiqueira on the inland coast and the Serra do Mar on the seaside coast, especially during the Eocene-Oligocene (Gontijo-Pascutti et al. 2012; Zalán 2012).

The largest grabens, 13 in number, are aligned in an east-northeast direction. The most prominent graben inland from the coast is known as Taubaté in São Paulo, and the most famous is the Guanabara graben, a low block by the sea where today, on the shore of the bay, the city of Rio de Janeiro is located. When the grabens are

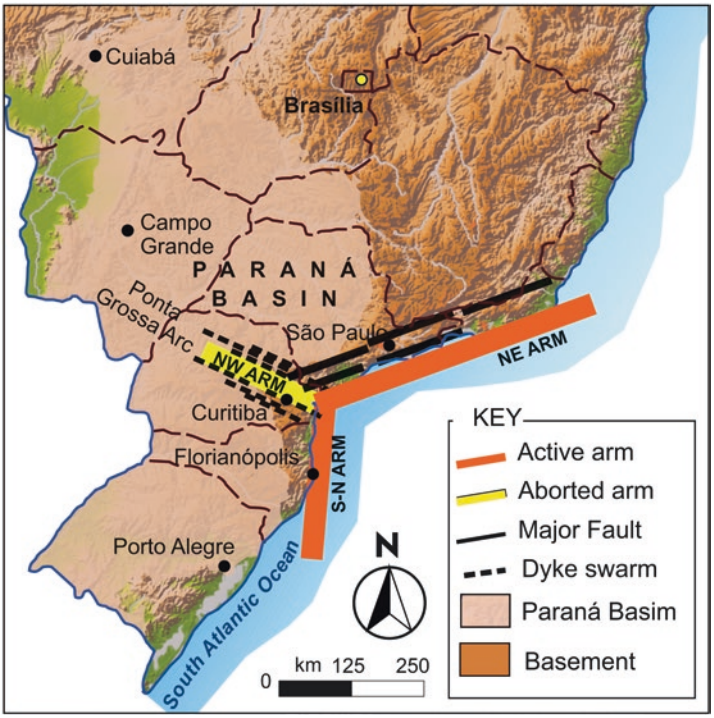

Fig. 2.12 The arms of a triple junction defined the direction of the coast of South-Southeast Brazil. The yellow arm has the same E-NE orientation as Serra do Mar and Mantiqueira. The red arm, with N-NE direction, coincides with the alignment of the Florianópolis faults and the southern coastline. Finally, the brown aborted arm, with a NW direction, identifies the Ponta Grossa Arc (Data from Almeida et al. 2012; Cartography by author)

situated by the sea, as in this case, the sandy coastal plain becomes more expansive, as also in the Ribeira de Iguapé, in São Paulo state, and in the graben of Paranaguá, in Paraná state.

In Paraná, the Serra do Mar exhibits elevations close to 1800 m at the edge of the Atlantic Plateau, locally called the Curitiba Plateau. In these highlands, minor grabens of the so-called Curitiba Basin have been installed, which are nothing less than the western extension of the Southeast Rifts System that characterizes the Serra do Mar in São Paulo and Rio de Janeiro. However, in Paraná, the escarpment of the uplifted blocks is more retreated toward the land than in the northernmost states due to the large Paranaguá graben to be located at the seaside (Gontijo-Pascutti et al. 2012). This retreat made the formation of the fluvial and marine plains of Paranaguá Bay possible. Therefore, the geomorphological section from Paranaguá to Curitiba is like a staircase from sea level to the top of the Serra do Mar escarpment.

The Serra do Mar ends in the southernmost region of Florianópolis. The stair graben pattern is evident only in the Itajaí region, in the north of SC state. In addition, the NE ridge direction seems to be driven by differential erosion and older

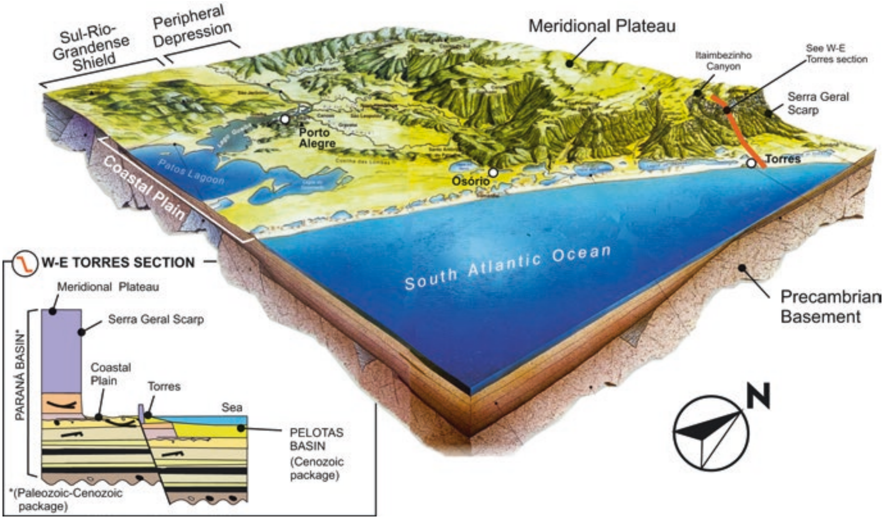

Fig. 2.13 Geomorphological configuration in the coastal region in the north of Rio Grande do Sul state, where the escarpment of the Meridional Plateau is dominant and then replaced by the range of large lakes from Porto Alegre to the very south. (Modified from Menegat et al. (2006b). By courtesy of Atlas Ambiental de Porto Alegre, 2006)

faults, such as those of the Cretaceous. The ridges have consistently become more eroded, and the frontline of the Atlantic Plateau escarpment, apparent in the northern segment, has disappeared. It has been replaced by the escarpment of the Meridional Plateau, which runs southward in the same direction as the front line – the 1400-m escarpment advances toward the shore, displaying the huge sedimentary-volcanic package of the Paraná Basin. From there, southward, the escarpment of the Meridional Plateau becomes pronounced and is called Serra Geral, which now dominates the coastal region until the northern coast of RS state (see Fig. 2.13).

2.6 The Coastal Province: The Rise and Fall of the South Atlantic Level in the Quaternary

In the southern coast of the Santa Catarina and the northern part of the Rio Grande do Sul, the escarpment of granitic and gneissic blocks of the Mantiqueira Province no longer dominates. Here, the coast is controlled by the escarpment of the Meridional Plateau, which corresponds to the uppermost units of the Paraná Basin that follows the coastline from the Laguna-Tubarão region in SC to Osório in RS (see Fig. 2.13). The narrow coastal plain between the escarpment and the beach, whose width ranges from 40 km to 15 km, is home to a chain of small lakes and lagoons. In the Osório region, the N-S direction escarpment inflects about 90° toward the West. The narrow coastal plain expands to 100 km in width and remains the same for 500 km to the south, where it reaches the border with Uruguay. Four large lagoons and lakes lie within this wider sandy coastal plain: Patos Lagoon (the largest in South America with 10,360 km^2), Mirim (3700 km^2), Mangueira (930 km^2), and Guaíba Lake (472 km^2).

This coastal plain is the onshore portion of the Pelotas offshore marginal basin – these offshore basins record depositional sequences under the Atlantic Ocean. There is a detailed record of the opening phase of the South Atlantic at its base, and toward the top, successive depositional sequences driven by marine transgressions and regressions over time. However, in the onshore portion, barrier-lagoon depositional systems have worked since the last four major marine transgressions and regressions during the Quaternary Period (Pleistocene and Holocene) (Dillenburg et al. 2009).

The first significant Quaternary transgression occurred 400,000 years ago, in the Pleistocene, when the sea level rose about 132 m compared to the current level (Dillenburg et al. 2009). In this transgressive event, the waters of the Atlantic Ocean reached the escarpment of the Meridional Plateau. The Coxilha das Lombas, a sandy ribbon 150 m high and 40 km long, NE oriented, which occurs in the eastern part of Porto Alegre, marks the position of the dune line installed by the lagoon-barrier system in this event (see Fig. 2.14) (Menegat et al. 2006a).

The second transgression occurred 32,000 years ago and delineated the coastal plain on the eastern flank of the Sul-Rio-Grandense Shield, the southernmost segment of the Mantiqueira Province. However, the coastal plain achieved its present configuration during the third major transgression, 125,000 years ago. During this event, Patos Lagoon and Guaíba Lake were formed. In the last transgression, 4600 years ago, when the sea rose about six meters above the current level, the lakes Mangueira and Mirim on the border with Uruguay were formed.

In the age of the Anthropocene, where gigantic cities and climate change predominate over the natural environment, knowledge of the past is essential to develop and understand future scenarios, whether on the coast or in the highlands. Today's landscapes and their resilience, e.g., to sea level rise or extreme climatic events that can result in landslides under certain geological conditions, are better understood when we put them into a timeline perspective, as presented in this chapter.

Old alluvial deposits are on the base of steeper slopes that identify recurrent downslope mass movements. The future climate scenarios of the southern Brazilian region, including in the Southeastern South America Region (SES), predict increasing mean and extreme precipitation and pluvial floods (IPCC 2021). Most of the lowlands in coastal plains or the graben floors of Serra do Mar are near steep escarpments, and mass movements could increase. Also, floods need attention to preserve wetlands to retain water flows, mainly in fluvial plains, as in the Porto Alegre Metropolitan area and Itajaí Valley (SC). Considering the rising sea level in the next period, we need to pay attention to terrains covered by marine water in the old times. The geomorphological configurations and records of past events are essential to better predicting possible dynamics with increasing sea levels. Also, natural vegetation plays a significant role in controlling the major water flows or floods that could occur either in escarpments or lowlands.

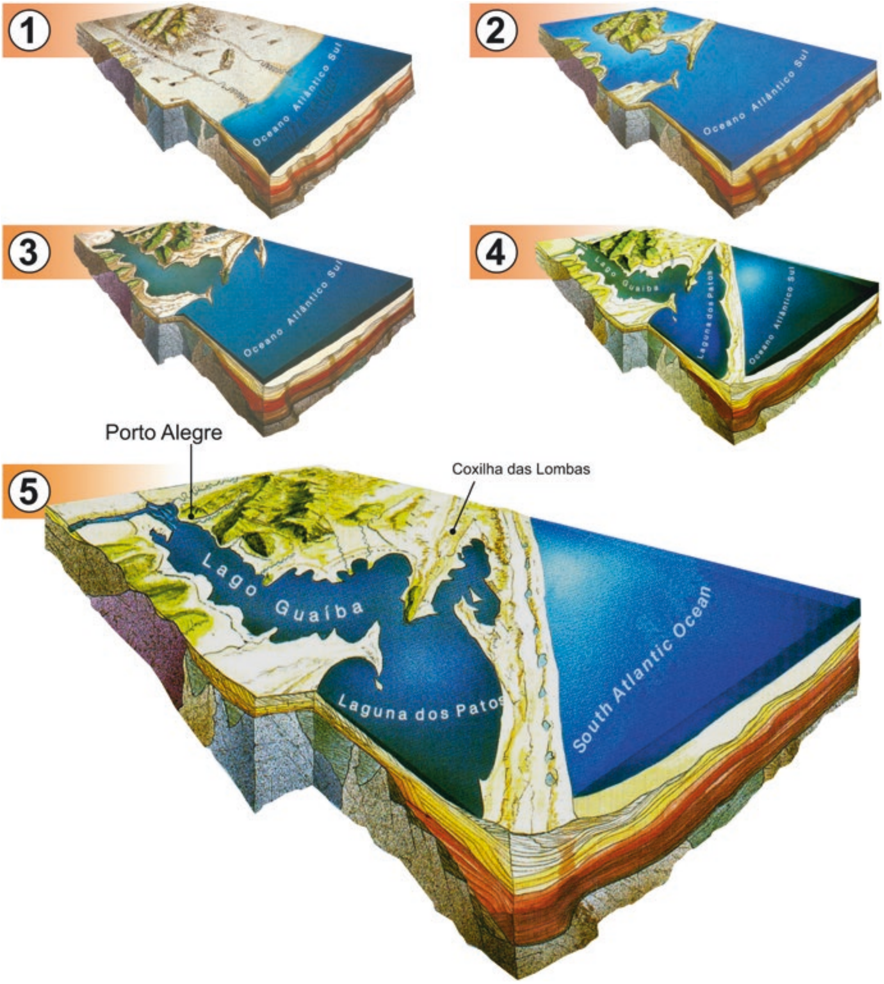

Fig. 2.14 Coastal evolution in the region of Porto Alegre, RS: (1) Before 400 thousand years (ky), sea level was about 70 m below today's level. (2) The first transgression, 400 ky. (3) The second transgression, 320 ky. (4) The third transgression, 125 ky. (5) The last transgression, 4,6 ky. (After Menegat et al. (2006a). By courtesy of Atlas Ambiental de Porto Alegre, 2006)

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Chapter 3
A Look into the Past: Fossils from the *Campos Sulinos* Region

Átila A. S. da Rosa, Leonardo Kerber, Felipe L. Pinheiro, and Joseline Manfroi

3.1 Introduction

The *Campos Sulinos*, i.e., the grasslands that dominate natural landscapes in the three southernmost states of Brazil, Rio Grande do Sul (SC), Santa Catarina (SC, and Paraná (PR), extend over different geological grounds in southern Brazil: igneous and metamorphic rock from the crystalline basement, fossiliferous sedimentary rocks from the Paraná Basin, volcanic rocks from the top of Serra Geral, and fluvial and coastal sedimentary deposits (Silva and Vaine 2001; Wildner et al. 2008, 2014; see also Menegat 2023, Chap. 2, this volume). This region witnessed important paleogeographic, paleoclimatic, and paleobiotic shifts in the last 300 million years, which will be summarized here (Fig. 3.1). Four major moments can be envisaged in this scenario in southern Brazil. The Permian started with a Gondwanic glaciation, but subsequent deglaciation led to sea level rise, the formation of an internal sea,

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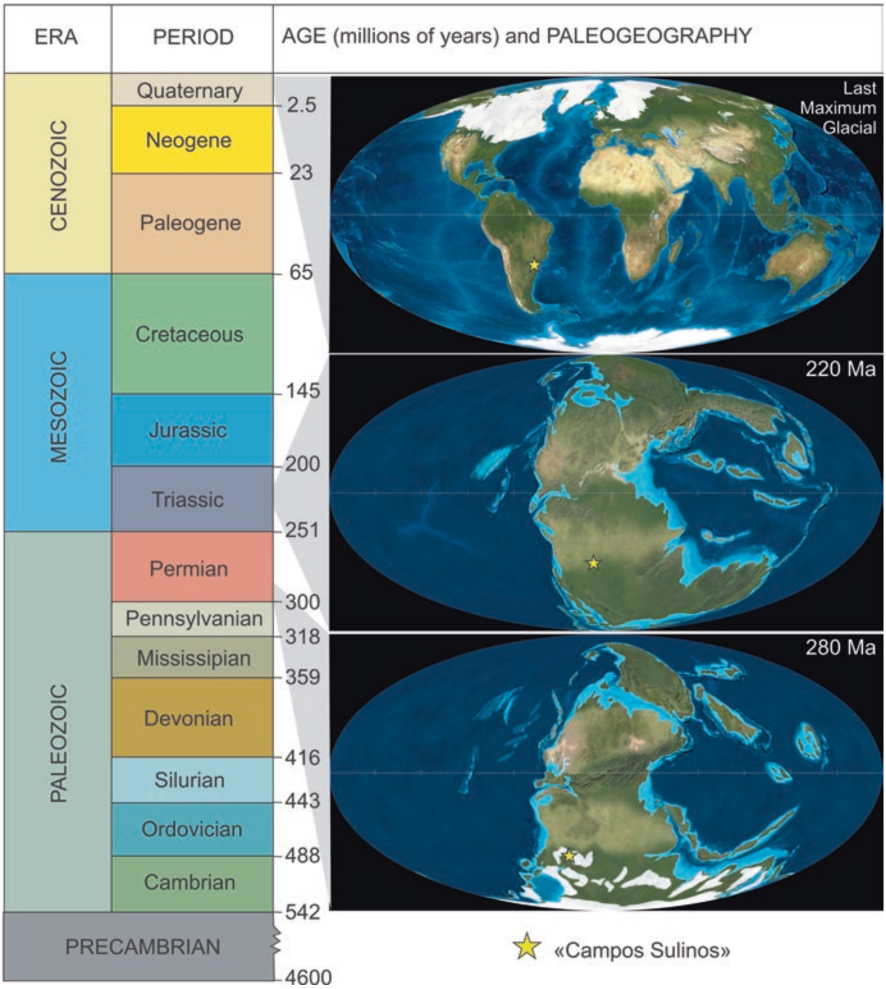

Fig. 3.1 Geological time scale and positioning of "*Campos Sulinos*" fossiliferous rocks in Permian (280 million years, Ma), Triassic (220 Ma), and Pleistocene (Last Maximum Glacial). (Global reconstructions after Ron Blakey)

and evolution to an alluvial plain in Pangean conditions. The Triassic witnessed the recovery of a massive extinction and development in alluvial plains in Pangean circumstances. The Late Jurassic and Early Cretaceous are known for their desert environments, prior to the breakup of South America and Africa. Finally, the glacial and interglacial cycles of the Pleistocene led to the onset of megamammals and large reptiles, later extinct between the latest Pleistocene and early Holocene, and the establishment of "*campos*"–forest mosaics.

3.2 Paleogeographic and Paleoenvironmental Reconstruction

Here we present the geobiological transformation over the last 300 million years (Ma), depicting four different periods: the Permian, Triassic, Jurassic-Cretaceous periods, and the Pleistocene Epoch (Fig. 3.1).

3.2.1 Permian

During the Permian, all land masses were gathered in a single, "C"-shaped supercontinent called Pangaea (see Fig. 3.1). This term was coined by Alfred Wegener in 1912 to designate the geological and paleobiological coalescence of present continents into a single supercontinent (Wegener 1912). According to current knowledge, the Pangaea was formed from the convergence of Laurentia, Baltica, and Gondwana during the late Carboniferous (Scotese and Golonka 1997). This supercontinent was bordered by two oceans, the Panthalassa and Tethys.

The Paraná Basin was part of the Gondwanan realm of Pangaea. Its geological history goes from glaciation at the beginning of the Permian period (Itararé Group) and later deglaciation, which led to sea level rise, coastal shift (Rio Bonito and Palermo Formations), and formation of an epicontinental sea (Irati Formation) in the mid-Permian (Holz et al. 2010). During the late Permian, continentalization started, leading to the formation of shallow lakes (Teresina Formation) and alluvial plains (Rio do Rasto Formation). The rocks from the Itararé Group are the record of glacial and postglacial environments, such as glaciomarine or glaciolacustrine settings (Vesely 2007; Weinschütz and Castro 2006). The record of Gondwanan glaciation in Brazil is preserved in some isolate sites, such as the Witmarsun and Salto glacial striations and Mafra dropstones (Santa Catarina), ruiniform relief at Vila Velha State Park (Paraná), and Itu Varvite (São Paulo) (Rocha-Campos 2002a, b; Melo et al. 2002; Pérez-Aguilar et al. 2008). Some outcrops are also known from Rio Grande do Sul.

The Rio Bonito Formation records lagoon-barriers deposited under sea level rise conditions, right after deglaciation. These more humid conditions led to the deposition of peat environments and coal formation (Lavina and Lopes 1987; Castro et al. 1999; Maahs et al. 2019). These rocks include leaf imprints of the *Glossopteris* Flora, which Alfred Wegener used as evidence of continental drift (Iannuzzi 2010; Jasper et al. 2009). The Palermo Formation is formed by mudstones and shales, due to a more prominent sea level rise, only recording rare marine microfossils (Simões and Rocha-Campos 1993). Outcrops are known from São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul.

The Irati Formation records an epicontinental sea with bituminous shales (Chahud et al. 2012). Its fossiliferous content, mainly characterized by crustaceans and mesosaurs, are worthy of mention, as they were also used as evidence of continental drift by Alfred Wegener (Araújo-Barberena et al. 2002; Cerri et al. 2020;

Oleofsen and Araújo 1983a, b, 1987a, b; Ricardi-Branco et al. 2009). Silicified logs are also present (Merlotti 2009). The preservation of almost complete skeletons of mesosaurs is related to winter storms and sea floor erosion (Lavina et al. 1991; Xavier et al. 2018). Outcrops are known from Paraná and Rio Grande do Sul states.

The Serra Alta Formation is composed of regressive facies of dark gray mudstones (Warren et al. 2015), recording bivalves (Matos et al. 2017a, b), ostracods (Bergue et al. 2020), and silicified logs (Merlotti 2009). The Teresina Formation is characterized by gray siltstones, intercalated with micritic carbonate and stromatolites, representing the transition from marine environments to marine zones with shallow water influenced by storms (Rohn 2001; Silva and Vaine 2001; Callefo et al. 2015), with fossils restricted to palynomorphs (Neregatto et al. 2008), pelecypods (Silva and Vaine 2001), ostracods (Bergue et al. 2020), and microbial mats (Callefo et al. 2015).

The Rio do Rasto Formation facies are diverse, with fluvial, aeolian, and lacustrine environments (Schemiko et al. 2014). Their sedimentary evolution indicates the formation of a large confined water body and the accumulation of a transgressive-regressive sequence at its lower portion, eventually recording storm conditions, while the progradational character of the upper portion led to the colmatation of the water body with deltaic and aeolian deposition (Warren et al. 2008). The Rio do Rasto Formation was considered Lopingian (Malabarba et al. 2003). However, a recent U-Pb age repositioned it to Guadalupian (Francischini et al. 2018).

3.2.2 Triassic

Still under the overall condition of continental agglutination, the Triassic witnessed a slight northern displacement of Pangea (Fig. 3.1), maintaining the paleoequator at the inflection of the boomerang-like structure (Golonka et al. 2018). At the end of the Triassic (Norian and Rhaetian), a massive bulging took place at that point, leading to the formation of a magmatic province, namely the Central Atlantic Magmatic Province (CAMP; Marzoli et al. 2018), which is related to the opening of the Atlantic Ocean and the extinction of several land vertebrates (Davies et al. 2017).

The Triassic record of the Paraná Basin is restricted to its southern portion, in Rio Grande do Sul. Here, two depositional packages were recognized, the Sanga do Cabral Supersequence, composed of the arenaceous rocks of the homonymous geological formation, and the Santa Maria Supersequence, integrating the Santa Maria and Caturrita formations (Zerfass et al. 2003). More recently, Horn et al. (2014) subdivided the Santa Maria Supersequence into third-order sequences: Pinheiros-Chiniquá (Ladinian?), Santa Cruz (early Carnian), Candelária (late Carnian to Norian), and Mata (Rhaetian?).

The Sanga do Cabral Supersequence records fine sandstones with intercalated intraformational conglomerates, deposited in broad alluvial plains (Da Rosa et al. 2009a, b), while the Santa Maria Supersequence (SMS) presents a more complex organization (Da Rosa 2015). The lower part of the SMS, i.e., the

Pinheiros-Chiniquá, Santa Cruz, and the lower portion of the Candelária sequences, records the intercalation of sandstones and fine-grained lithologies, deposited at low energy, high sinuosity rivers, representing channels, levees, overbank deposits, shallow and temporary lakes, loess, and paleosols (Da Rosa et al. 2004a, b, 2005; Horn et al. 2013). On the other hand, the upper portion of the SMS shows a predominantly sandy deposition in high energy, low sinuosity rivers, with channels and overbank deposits (Müller et al. 2015).

3.2.3 Jurassic/Cretaceous

The time interval between the end of the Jurassic and the beginning of the Cretaceous is characterized by the continuation of the Pangaea breakup, with main interest in the separation of South America and Africa circa 135 Ma ago. In the Paraná Basin, the Guará Formation consists of fine to conglomeratic sandstones of whitish to reddish color, with trough cross-stratification from small to large size and horizontal lamination. The facies associations characterize fluvial to fluvio-aeolian deposits, with a distinctive change throughout its exposure, the northern part consisting of facies associations of braided fluvial systems and the southern part showing a tendency to replace the predominant fluvial facies by aeolian associations (Scherer and Lavina 2005). These fluviatile-desertic sandstones are correlated to the Tacuarembó Formation in Uruguay and placed at the end of the Jurassic based on their faunal content (see Sect. 3.3.3).

3.2.4 Pleistocene

The main Cenozoic units from Rio Grande do Sul are restricted to the Quaternary Period (2.58 million years ago to the present), more precisely between the Middle Pleistocene and the Holocene. During the Pleistocene, the continents were already organized in their present condition (Fig. 3.1), with rapidly changing environments due to glacial cycles and subsequent sea level fall, the imposition of dry climates, and the shift of river profiles and coastal lines (Golonka 2009). The Pleistocene deposits, mostly formed in fluvial environments, are found in western RS (WRS – Alegrete, Quaraí, and Uruguaiana) (Lopes et al. 2020), central region (Caçapava do Sul, Pantano Grande), and Coastal Plain (CPRS – Santa Vitória do Palmar). In addition to these locations, there are several others with sparse records, such as São Gabriel and Jaguarão. Different methodologies, such as Carbon-14 (^{14}C), Accelerated Mass Spectrometry (AMS), Electron Spin Resonance (ESR), and Optically Stimulated Luminescence (OSL), have been applied to time-calibrate fossils and Pleistocene sediments. Radiometric ages from WRS (Touro Passo Creek, Uruguaiana; Quaraí River, Quaraí; Sanga da Cruz and Ibicuí River, Alegrete) are placed between ~42 and 10 ka (Bombin 1976; Miller 1987; Kotzian et al. 2005;

Milder 2000; Ribeiro and Scherer 2009; Kerber et al. 2011a, b, c), while deposits from the CPRS include older sediments. Chuí Creek sedimentary strata (Santa Vitória Formation, Santa Vitória do Palmar) were deposited between ~190 and ~30 ka, with most fossils dated between 50 and 30 ka (Lopes et al. 2014a, b, 2019, 2020). The fossils from onshore deposits found in Balneario Hermenegildo (Santa Vitória do Palmar) are even older, dated between 650 and 18 ka (Lopes et al. 2010). Concerning the record of tetrapods, the fossils found in these locations show a certain taxonomic uniformity (although some peculiarities are observed; see Sect. 3.4) and mostly represent fossils of large mammals (Mammalia) known as the Pleistocene megafauna. However, other small vertebrates, such as lizards, birds, and fishes, are also recorded.

3.3 Biodiversity and Paleoecological Reconstruction of Fauna and Flora

Here, we summarize the faunistic (tetrapods) and floristic biodiversity and paleoecological inferences of the studied time intervals, i.e., Permian, Triassic, Jurassic/Cretaceous, and Pleistocene.

3.3.1 Permian

Almost all Permian rocks in the *Campos Sulinos* region have a fossil record restricted to fish, invertebrates and/or plant fossils. However, exceptions are the Irati and Rio do Rasto formations, which present tetrapods in a more complex food chain. Few fossils are known from the Itararé Group, and they consist of invertebrates (Matos et al. 2017a; Neves et al. 2014; Taboada et al. 2016), fish fragments and ichnofossils, such as annelid and trilobite trackways (Netto et al. 2009; Lima et al. 2015; Wilner et al. 2016; Noll and Netto 2018). The Irati Formation is remarkable for its exceptional record of mesosaurs, i.e., parareptilles adapted to an aquatic way of life, such as thickened bones (especially ribs) and characteristic teeth. Three mesosaur species were proposed for the Irati Formation, *Mesosaurus brasiliensis*, "*Stereosternum tumidum*", and "*Brazilosaurus saopaolensis*"). Piñeiro et al. (2021), however, recognized only the former as valid. Mesosaurs seem to have fed on fish and pygocephalomorph crustaceans in the Irati-Whitehill Sea.

A complex and diversified fauna inhabited the aquatic environments associated with the deposition of the Rio do Rasto Formation. The unit already yielded abundant actinopterygian remains, even though those are often represented by fragmentary bones and isolated "paleonisciform" scales. Exceptions to these highly transported, mainly uninformative materials come from the Serrinha Member, known for its representativeness of low-energy depositional environments (e.g., Milani et al. 2007). Perhaps the best-preserved actinopterygian so far recovered from the Rio do Rasto Formation is the bizarre *Paranaichthys longianalis*, a laterally flattened fish with flamboyant anal fins (Dias 2012). *Paranaichthys* is known solely from its holotype, a superbly preserved specimen recovered in Paraná state. *Rubidus pascoalensis*, another Rio do Rasto actinopterygian known from a complete specimen, had a more elongated body, displaying several rows of diamond-shaped scales (Richter 2002).

The diagnostic nature of isolated shark teeth and fin spines made it possible to recognize three nominal shark species for the Rio do Rasto Formation, all known by fragmentary specimens. Two of these, *Xenacanthus ragonhai* and *Triodus richterae* (Pauliv et al. 2014, 2017), belong to the Xenacanthiformes, eel-like sharks with long and low dorsal fins and strong denticulated fin spines. Xenacanthiform teeth are easily recognized by their tricuspid crowns, with long lateral cusps flanking a smaller central one. Recent findings suggest that xenacanthiforms may be at least partially responsible for producing the exceptional coprolite concentrations found in Rio do Rasto outcrops (e.g., Dentzien-Dias et al. 2012a, b). A third shark species, *Sphenacanthus riorastoensis*, belongs to the enigmatic Sphenacanthidae, and is only known from isolated fin spines (Pauliv et al. 2012).

Sharks were not the apex predators in mid- and late-Permian freshwater bodies. At that time, this role was played by the Temnospondyli, an extraordinarily diverse clade of early-diverging tetrapods commonly referred to as “amphibians” (Schoch 2013). With a wide range of sizes and an obligate carnivorous diet, temnospondyls may have played an ecological role similar to that of modern-day crocodilians, even though several representatives were adapted to feed in terrestrial environments (Clack 2012). Several temnospondyl nominal species are known from the Rio do Rasto Formation, this being by far the best-represented group in this sedimentary unit. Like modern caimans, some Rio do Rasto temnospondyls, such as *Rastosuchus hammeri* (Dias et al. 2020) and *Parapytanga catarinensis* (Strapasson et al. 2015) had short and broad snouts, while the bizarre *Australerpeton cosgriffi* and *Bageherpeton longignathus* had exceptionally long and slender snouts, completely filled with small (but sharp) needle-shaped teeth (Dias and Barberena 2001; Pacheco et al. 2016; Azevedo et al. 2017).

Synapsids, the mammal forerunners, were abundant during the Permian period, dominating most land ecosystems and occupying several ecological roles that ranged from primary consumers to apex predators. In the Rio do Rasto Formation, herbivore synapsids belong to the clade Anomodontia. Anomodonts were diverse forms of mainly tusked herbivores that prospered during most of the late Permian and Triassic times. Early-diverging anomodonts are rare in the fossil record. Among these, the most striking is certainly *Tiarajudens eccentricus*, a saber-toothed pig-sized animal known by an almost complete skull and some postcranial remains from a Rio do Rasto Formation outcrop. Besides long canines, *Tiarajudens* had strong molariforms adapted to macerate vegetation (Cisneros et al. 2011, 2015). The saber-like canines of *Tiarajudens* likely evolved as display structures, perhaps also being used during intraspecific agonistic interactions, similar to what is seen today in musk deers (Cisneros et al. 2015).

Dicynodontia, the most diverse anomodont subclade, has two representatives in the Permian of Brazil. Among these, the best-known is *Rastodon procurvidens*, a diminutive (~40 cm long) dicynodont that lacked teeth except for two small forward-directed banana-shaped tusks (Boos et al. 2016; Simão-Oliveira et al. 2019). *Rastodon* is known from a single, superbly preserved specimen, including an almost complete skull and several postcranial bones. As can be extrapolated from other Permian dicynodonts, *Rastodon* was probably gregarious and excavated burrows for protection (Simão-Oliveira et al. 2019). The second Rio do Rasto Formation dicynodont, *Endothiodon* sp., is known only from a crushed and incomplete skull from Paraná (Barberena and Araújo 1975; Boos et al. 2013). Despite fragmentary, *Endothiodon* is a key taxon to understanding Rio do Rasto Formation geochronology, allowing a direct correlation with the better-studied South African Karoo Basin.

The remaining synapsids recovered from the Rio do Rasto Formation belong to the clade Dinocephalia. Medium to large animals, dinocephalians apparently had a wide range of feeding habits and were first reported from the Rio do Rasto Formation through isolated teeth and jaw fragments (Langer 2000). Only in 2012 the first reasonably complete specimen was introduced, the complete (albeit crushed) skull of the medium-sized carnivore *Pampaphoneus biccai* (Cisneros et al. 2012). This specimen so far represents the largest land predator of the Brazilian Permian, probably occupying an apex position in its food chains. A second, more complete *Pampaphoneus* specimen was recently recovered from the same outcrop where the holotype was found (Costa Santos et al. 2023). This new specimen contributes with information on the anatomy of this carnivorous dinocephalian. Still unpublished, this specimen will contribute with information on the anatomy of this carnivorous dinocephalian. The Rio do Rasto Formation also yielded a single herbivorous dinocephalian specimen (Boos et al. 2015). Albeit not sufficiently complete to allow a specific attribution, the material confirms the presence of the dome-headed tapinocephalid dinocephalians in the Brazilian Permian. A summarized scenery of the Rio do Rasto Formation is available in Fig. 3.2.

The taphoflora preserved in the Rio do Rasto Formation deposits is characterized by the latest records of the *Glossopteris* Flora, which dominated most environments during the Permian Period, before the formation of desertic landscapes at the end of the Paleozoic. The *Glossopteris* Flora represents one of the most important paleofloras preserved over geological time. In addition to its wide paleogeographic distribution, which attests to the continental drift proposed by Alfred Wegener in 1912, this flora also witnessed the most important environmental and climatic changes that occurred in the course of the Permian Period, from the transition of the icehouse to the greenhouse stage and the aridization of previously moist environments, culminating in the Earth's greatest mass extinction.

The main floristic elements that characterize the *Glossopteris* Flora were diagnosed mainly through impressions of leaves and stems of *Glossopteris*, *Gangamopteris*, *Rubidgea*, and *Buriadia* (Guerra-Sommer and Cazzulo-Klepzig 2000a, b). Other groups still present in today's environments, such as the lycophytes *Cyclodendron* sp. (Herbst 1986) and *Lycopodiopsis* sp. (e.g., Martins and Sena-Sobrinho 1951; Ferraz et al. 2021), the sphenophyte *Shenophylum* sp. (e.g., Rohn

Fig. 3.2 Permian. Faunistic elements depicted, from front to back: *Australerpeton*, *Bageherpeton*, *Rastodon*, *Tiarajudens*, *Provelosaurus*, *Pampaphoneus*, and indeterminate tapinocephalian. (Floristic records: Equisetales and Cycadaceae. Artwork: Voltaire Dutra Paes Neto)

and Rösler 1990; Iannuzzi 2010), and the pteridophytes *Pecopteris* sp. (e.g., Cazzulo-Klepzig 1978; Rohn and Rösler 1986; Ferraz et al. 2021), *Schizoneura* sp. (e.g., Cazzulo-Klepzig 1978; Cazzulo-Klepzig and Correia 1981), *Dichophyllites* sp. (Bortoluzzi 1975; Rohn 1988), and *Paracalamites* sp. (Bortoluzzi 1975; Rösler and Rohn 1984), have also been documented.

Although vegetation records in the Rio do Rasto Formation predominantly indicate hygrophilic and mesophilic habits (Rohn 1988), the slow process of aridization during this period was documented through the reduction of floristic diversity. Records of pteridophytes become rarer, lycophytes are represented only by arborescent and shrubby forms, and *Glossopteris* species show changes in their leaf structure, with a reduction in limb dimensions and secondary venation of leaves. These signs suggest a warm and semi-arid climate, with long dry seasons alternating with rainy seasons of moderate rainfall (Guerra-Sommer and Cazzulo-Klepzig 2000a, b).

Due to environmental disturbances in the Permian (Guadalupian), including forest fires (Manfroi et al. 2015), there was a significant change in the floristic landscape, also affecting the cohabiting fauna. For example, evidence of insect–plant interactions in these deposits was seen in *Glossopteris* sp. with damaged leaf edges, indicating phytophagy and climatic cyclicity (Rohn 1988). Likewise, herbivorous vertebrates that fed on the existing vegetation on the edges of Permian lakes suffered from the reduction of available plant biomass, such as recorded for the *Equisetales*. This may have caused a disturbance in the entire food chain, which, along with other factors, later resulted in the end of the Paleozoic Era.

3.3.2 Triassic

The tetrapod biodiversity of the Brazilian Triassic is summarized into five assemblage zones (AZs) of biostratigraphic relevance (Schultz et al. 2020). Each AZ can be regarded as a different fauna. The AZs are organized in time, so that their succession represents the evolution of land communities from the devastated, postextinction Early Triassic environments toward the mature, stable Late Triassic ecosystems in which the first dinosaurs dwelt.

The diverse ecomorphological adaptations present in vertebrates from each AZ suggest the presence of complex ecological interactions and food chains during the time intervals recorded in the southern Brazilian fossil record (see evidence of trophic relationships in Schwanke and Kellner 2009). The earliest Brazilian Triassic assemblage zone is the *Procolophon* AZ. Albeit still poorly sampled, this AZ has recently been shown to hold an important and relatively diverse tetrapod fauna. The archosauromorph *Teyujagua paradoxa* and temnospondyl amphibians (e.g., *Sangaia lavinai* and *Tomeia witecki*) played their roles as carnivores in Early Triassic times (Pinheiro et al. 2016, 2019; Eltink et al. 2016). At the same time, the parareptiles *Procolophon trigoniceps* and *Oryporan insolitus* were probably omnivore/herbivore animals (Pinheiro et al. 2021). The proterosuchid archosauriforms and the tanystropheid *Elessaurus gondwanaoccidens* were probably specialized faunivores (De-Oliveira et al. 2020, 2022). Although inferring Early Triassic food chains is not an easy task, the increasing number of specimens recovered will certainly improve our knowledge of ecosystem dynamics in this period.

The second, younger Brazilian Triassic assemblage zone is the *Dinodontosaurus* AZ (Schultz et al. 2020). This AZ records a more complex ecosystem, where huge archosaurs such as *Prestosuchus chiniquensis* (~12 m long) were the apex predators. In contrast, smaller archosaurs (e.g., *Decuriasuchus quartacolonia*, *Pagosvenator candelariensis*, *Archeopelta arborensis*, and indeterminate proterochampsids and rauisuchians) may have played a secondary role as carnivores. In this AZ, non-mammaliaform cynodonts become very diversified in the fossil record of Rio Grande do Sul. The herbivore/omnivore cynognathians are represented by several traversodontids: *Massetognathus ochagaviae* and *M. pascuali*, *Traversodon stahleckeri*, *Protuberum cabralense*, *Luangwa sudamericana*, and *Scalenodon ribeiroae* (von Huene 1936; Abdala and Teixeira 2004; Liu et al. 2008; Reichel et al. 2009; Melo et al. 2017). The last two taxa have coeval species recorded in African Triassic strata. Probainognathians (mostly carnivore/insectivore cynodonts) include *Chiniquodon theotonicus*, *Protheriodon estudianti*, *Candelariodon barberenai*, *Aleodon cromptoni,* and *Bonacynodon schultzi* (von Huene 1936; Bonaparte et al. 2006; Oliveira et al. 2011; Martinelli et al. 2016, 2017a). Dicynodonts were herbivores of large (*Stahleckeria potens*) and medium size (*Dinodontosaurus*) (von Huene 1935; Schultz et al. 2020). The owennetid parareptile *Candelaria barbouri* seems to have been faunivorous, probably insectivorous.

The next assemblage zone (*Santacruzodon* AZ) has a still scarce fossil record, which can be attributed to sampling bias or a possible co-occurrence with the older *Dinodontosaurus* AZ. This biozone has produced a number of traversodontid and probainognathian cynodonts, but rauisuchian and proterochampsid archosaurs are also present. The traversodontid *Santacruzodon hopsoni*, which names the AZ, is the most abundant cynodont (Abdala and Ribeiro 2003), but there are also records of *Massetognathus ochagaviae*, *Menadon besairiei*, and the probainognathians *Santacruzgnathus abdalai* and *Chiniquodon* sp. (Melo et al. 2015; Martinelli et al. 2016; Schmitt et al. 2019). Interestingly, the Malagasy *Menadon besairiei* is a Triassic cynodont with hypsodont postcanines (indicating the presence of specialized adaptations in herbivores as a result of the arid Triassic environments), previously described from the 'Isalo II' group of Madagascar (Melo et al. 2015, 2019). Aside from indeterminate proterochampsids (Hsiou et al. 2002; Raugust et al. 2013; Ezcurra et al. 2015), a single large-sized predator archosaur was recorded for the *Santacruzodon* AZ. *Dagasuchus santacruzensis*, known solely from a fragmentary pelvis (Lacerda et al. 2015), was a medium-sized rauisuchian, probably very similar to its "cousin" *Prestosuchus chiniquensis*.

The *Hyperodapedon* AZ was probably the most diverse assemblage zone, in which several carnivores disputed the same geographic area (Garcia et al. 2019). Archosaurs such as proterochampsids, rauisuchians, silesaurids, and early dinosaurs (herrerasaurids and basal sauropodomorphs) were the main predators. The most common herbivores were rhynchosaurs, but cynodonts were also present, as well as clevosaurid sphenodontians. Procolophonians were never recorded from this time interval, but a new taxon is currently under study (Silva-Neves in prep). Regarding the cynodonts, the cynognathians are represented by the traversodontid *Exaeretodon riograndensis*, one of the most abundant fossils of this association, *Gomphodontosuchus brasiliensis*, represented by few remains, and the recently described *Santagnathus mariensis* (von Huene 1928; Hopson 1985;

Abdala et al. 2002; Schultz et al. 2020; Schmitt et al. 2023). Probainognathians are more diverse and include the enigmatic *Charruodon tetracuspidatus*, the large body-sized ecteniid *Trucidocynodon riograndensis*, and the small prozostrodontians, probably insectivorous or carnivores, *Prozostrodon brasiliensis*, *Therioherpeton cargnini*, and *Alemoatherium huebneri* (Barberena et al. 1987; Abdala and Ribeiro 2000; Oliveira et al. 2010; Martinelli et al. 2017b; Kerber et al. 2020, 2022; Stefanello et al. 2023). In addition, two other cynodonts may be included in this AZ, or alternatively in the younger *Riograndia* AZ, or even at an as-yet-unknown interval: the traversodontid *Siriusgnathus niemeyerorum* and the probainognathian *Agudotherium gassenae*, both recovered from outcrops in Agudo municipality in central RS, but without index fossils so far (Pavanatto et al. 2018; Miron et al. 2020; Martinelli et al. 2020). The fossil content of these two localities appears to be endemic when compared to other Brazilian Triassic outcrops.

Archosauromorph diapsids were also a major component of the *Hyperodapedon* AZ. As mentioned before, the most abundant herbivores were the rhynchosaurs, bizarre pig-sized early archosauromorphs bearing beak-like projections on their jaws. Two rhynchosaur taxa are known for this AZ: the widespread genus *Hyperodapedon* and the smaller, more recently described species *Teyumbaita sulcognathus* (Montefeltro et al. 2010). The bulky aetosaurs were armored omnivore archosaurs, represented by the taxa *Aetosauroides scagliai* and *Aetobarbakinoides brasiliensis* (e.g., Desojo et al. 2012; Brust et al. 2018; Paes-Neto et al. 2021). Aside from these species, *Hyperodapedon* AZ archosauromorphs are also represented by the proterochampsids *Rhadinosuchus gracilis* (von Huene 1938), *Cerritosaurus binsfeldi* (Price 1946) and *Proterochampsa nodosa* (Barberena 1982), as well as the rauisuchian *Rauisuchus tiradentes* (von Huene 1938). Most interestingly, the *Hyperodapedon* AZ preserves a wealth of early dinosaurs, most of which being forerunners of the long-necked sauropods, such as the sauropodomorphs *Buriolestes schultzi* (Cabreira et al. 2016), *Saturnalia tupiniquim* (Langer et al. 1999), *Bagualosaurus agudoensis* (Pretto et al. 2018), and *Pampadromaeus barberenai* (Cabreira et al. 2011). Typical carnivores are represented by the Herrerasauridae, medium-sized apex predators bearing sharp teeth and hooked hand claws (*Staurikosaurus pricei* and *Gnathovorax cabreirai*) (Colbert 1970; Pacheco et al. 2019). Finally, *Ixalerpeton polesinensis* was a small dinosaur-related gracile archosaur, recently proven to be akin to the pterosaurs (Cabreira et al. 2016; Ezcurra et al. 2020). Figure 3.3 illustrates some taxa of the *Hyperodapedon* AZ.

Unlike the Carnian strata, the Norian fossil record of synapsids in the subsequent *Riograndia* AZ is characterized by the return of large-sized dicynodonts to the Brazilian fossil record. The only known taxon is the stahleckeriid *Jachaleria candelariensis* (Kannemeyeriiformes), which represents one of the last South American dicynodonts (Araújo and Gonzaga 1980; Martinelli et al. 2020). Although almost all fossils point to fully terrestrial forms, two aquatic vertebrates are present: a fragmentary interclavicle of a Stereospondyli (Dias-da-Silva et al. 2009) and part of a snout of an indeterminate phytosaur (Kischlat and Lucas 2003). On the other hand, except for putative records of traversodontids (Ribeiro et al. 2011) plus the records mentioned above (pending further geochronological studies), the confident fossil

Fig. 3.3 Triassic. Faunistic elements, from front to back: *Hyperodapedon*, *Exaeretodon*, *Gnathovorax*, and *Dynamosuchus*. (Floristic records: *Dicroidium*, Cycadaceae. Artwork: Márcio L. Castro)

record of cynodonts is exclusively of small prozostrodonts, which include the "ictidosaur" *Riograndia guaibensis*, and the tritheledontids *Irajatherium hernandezi*, *Botucaraitherium belarminoi*, and *Brasilodon quadrangularis*, the sister-group to Mammaliaformes (Bonaparte et al. 2003, 2005; Martinelli et al. 2005, 2017c; Soares et al. 2011, 2014; Kerber et al. 2022). These forms are important for understanding the origin and early evolution of Mammaliaformes and, consequently, provide evidence for the reconstruction of mammalian history.

Dinosaurs were also present in the *Riograndia* AZ strata, albeit were less diversified than in the older *Hyperodapedon* AZ. Three dinosaur taxa are currently known, two of them belonging to the Sauropodomorpha (*Macrocollum itaquii* and *Unaysaurus tolentinoi*) (Leal et al. 2004; Muller et al. 2018), while the third species (*Guaibasaurus candelariensis*) has disputed affinities (Bonaparte et al. 1999; Langer et al. 2010). Other *Riograndia* AZ archosauromorphs include the pterosauromorphs *Faxinalipterus minima* and *Maehary bonapartei* (Bonaparte et al. 2010; Kellner et al. 2022) and the dinosaur-like silesaurid *Sacisaurus agudoensis* (Ferigolo and Langer 2021).

The Triassic period has witnessed one of the main vegetation transitions in the Earth's history, with environments dominated by the *Dicroidium* Flora gradually replacing the *Glossopteris* Flora, abundant during the Permian. The *Dicroidium* Flora was composed of plants better adapted to the new climatic conditions, significantly warmer and drier than in the previous period. Among them are the Corystospermales (*Xylopteris, Dicroidium,* and *Jonstonia*), which, despite being morphologically very similar to ferns (pteridophytes), produced seeds (spermatophytes) as the gymnosperms (Guerra-Sommer et al. 1999; Pankaj et al. 2014).

In RS deposits, remarkable fossiliferous assemblages that reveal the taphoflora, mainly of conifers of the group *Araucarioxylon*, are associated with the last fossil records of Triassic tetrapods. The herbivores at the time probably fed on shrubs and small arboreal plants of the *Dicroidium* Flora. The changes that occurred in the composition of the flora due to lower rainfall and higher temperatures are pointed out as one of the reasons for the substitution of the cynodont and dicynodont fauna, which did not adapt to the new vegetation, thus leaving room for the domain of rhynchosaurs and first dinosaurs (Guerra-Sommer et al. 1998; Guerra-Sommer and Cazzulo-Klepzig 2007; Langer et al. 2007; Schultz and Langer 2007; Horn et al. 2014).

The Triassic plains in western Gondwana (where southern Brazil is located today) were filled not only by plant groups that are now extinct, such as Corystospermales, but also by plants that still have extant representatives, e.g., the phyllicophytes (*Todites, Clapophlebis*, and *Asterotheca*), ginkgophytes (*Ginkoites, Baiera*, and *Stenorachis*), sphenophytes (*Neocalamites*), conifers (*Araucarioxylon, Podozamites,* and *Rissikia*), and cycads (*Pseudoctenisi, Otozamites,* and *Taeniopteris*). This taphoflora is found in the fossil record through the impression of fronds, leaves, and stems in clayey sediments and silicified stems in clayey and sandy sediments (e.g., Guerra-Sommer et al. 1999; Da Rosa et al. 2009a, b; Barboni and Dutra 2015). These distinct taphonomic and depositional processes have been the subject of debate up to the present. The so-called *Dicroidium* Flora, preserved through normally articulated impressions, is associated with a low-energy depositional environment. On the other hand, the Coniferous Flora, or "*Araucarioxylon* Flora", is represented by phytofossils of silicified stems associated with high energy deposition. The Coniferous Flora was composed of floristic elements with overall small leaves, such as the Araucariaceae, Taxodiaceae, and Cheiropodiaceae. The difficulty in performing the biostratigraphy insertion of this palaeoflora results from the fact that the fossiliferous record is rarely found in situ. However, Guerra-Sommer et al. (1999) suggest that the *Dicroidium* Flora and the Coniferous Flora preserved in RS deposits were contemporary floristic communities and belonged to the same depositional system, but preserved in different faciologies. The *Dicroidium* Flora is related to a depositional system proximal to the fluvial plain, due to its hygromesophilic features, and the *Araucarioxylon* Flora, with mesoxerophilic features, is associated with distal deposits of the flooding plain.

Regarding the conifer taphoflora in the Triassic deposits of RS, there are very few records of leaf branches of Araucariaceae (Crisafulli and Dutra 2009; Barboni and Dutra 2013), and all other records of this conifer flora are thus far only constituted by silicified wood, with no other records of associated macro- or microfossils (Horn et al. 2014). This assembly of silicified woods of *Araucarioxylon* preserved in conglomeratic sandstones that characterize the Mata Sequence represents one of the most important paleobotanical sites in South America and, although its deposition is evidently associated with high-energy fluvial events, being an allochthonous taphocoenosis, the analysis of the anatomical structures of these woods corroborates a climate with low seasonality as inferred for the Triassic in these latitudes (Pires and Guerra-Sommer 2004; Pires et al. 2005; Dos Santos et al. 2023).

3.3.3 Juro-Cretaceous

The Brazilian Jurassic is predominantly represented by aeolian sedimentary units, so the scarcity of body fossils is remarkable. As such, most of what we know about Jurassic faunas that thrived in southern Brazil comes from ichnological evidence – especially footprints and burrows (e.g., Dentzien-Dias et al. 2007, 2012a, b; Francischini et al. 2015, 2017). These have been recovered from the Guará Formation (Upper Jurassic), a geographically restricted unit with a predominance of aeolian and fluvial deposition (Scherer and Lavina 2005). The Guará Formation crops out in the southwestern portion of Rio Grande do Sul, with aeolian exposures concentrated toward the south (Scherer and Lavina 2005). However, it is noteworthy that the Guará Formation has a lateral correlation with the Uruguayan Tacuarembó Formation, from which a large number of somatic (i.e., body fossils) occurrences have already been reported (e.g., Perea et al. 2009; Soto et al. 2021).

Dinosaurs are the main components of the Guará Formation ichnoassemblage. Their footprints are found in both sand dune and sand sheet deposits (Dentzien-Dias et al. 2012a, b), especially within the boundaries of Santana do Livramento and Rosário do Sul municipalities. The first Guará Formation dinosaur footprints were formally reported by Scherer and Lavina (2005). Subsequently, Dentzien-Dias et al. (2007) conducted the first detailed assessment of dinosaur tracks and small-sized vertebrate burrows. These authors recognized a diverse assemblage composed of sauropods, theropods, and ornithopods. In a later contribution, Dentzien-Dias et al. (2012a, b) quantified Guará Formation occurrences, recognizing the presence of 60 dinosaur tracks. Footprints from which a conclusive identification can be made reveal an ichnoassemblage dominated by sauropods ($n = 22$) and theropods ($n = 15$), with a smaller contribution of ornithopods ($n = 6$).

The most recent contribution to the knowledge of the southern Brazilian Late Jurassic faunas was the recognition by Francischini et al. (2017) of the presence of ankylosaur tracks in a Guará Formation outcrop. Besides the scarcity of ankylosaur fossils in South America, the Guará Formation occurrence represents the oldest record of this clade in the western portion of Gondwana. The discovery of this new and unexpected ichnotaxon highlights the underexplored potential of the Guará Formation in revealing clues from the elusive Brazilian Jurassic faunas.

3.3.4 Pleistocene

The fossil record of Pleistocene tetrapods, especially mammals, shows a mixture of taxa from lineages with different biogeographic origins: mainly forms that evolved in South America during the Paleogene (in addition to caviomorphs, of African origin) and Neogene, and tetrapods that immigrated from the northern hemisphere (Central and North America) during the Great American Biotic Interchange (GABI) (see Woodburne 2010; Goin et al. 2012; Forasiepi et al. 2014; Carrillo et al. 2015; O'Dea et al. 2016). This biogeographic event, which is perhaps primarily responsible for the emergence of the modern fauna of the South American continent (Carrillo et al. 2015), was the biotic interchange between South America and North and Central America. It began during the Late Miocene (~10–7 Ma), with the arrival of the first immigrants (i.e., procyonids and cricetid rodents, also called "island hoppers", in reference to the fact that the isthmus was not fully formed), and was intensified between the end of the Pliocene (2.7 million years) and the Pleistocene (Woodburne 2010; Goin et al. 2012; O'Dea et al. 2016). Before the Pliocene, terrestrial organisms could not pass freely between these continents because the Isthmus of Panama had not yet been fully formed. As a result, South America was virtually isolated from the northern hemisphere by land routes during part of the Cenozoic. After the formation of this terrestrial connection, several organisms migrated from one region to another, significantly modifying the biotic composition of the continent's ecosystems. This mixture of organisms resulted in the so-called South America Pleistocene Megafauna (Fig. 3.4), characterized by the presence of several large-sized mammals (>300 kg), such as giant sloths, glyptodonts, pampatheres, toxodonts, macrauchenias, horses, cervids, large carnivores, and mastodonts, among others. Apart from a few exceptions, megamammals disappeared at the end of the Pleistocene. So far, all mammals found in RS are placentals, as marsupials are still unknown in the fossil record. These placentals represent four large groups: Xenarthra, Laurasiatheria, Euarchontoglires, and Afrotheria (Asher et al. 2009). Some iconic fossils from the Pleistocene Megafauna are shown in Fig. 3.4.

Concerning autochthonous South American mammals present in the Pleistocene of RS, a first group is Xenarthra the only placental lineage with extant species originating in South America. This is one of the most emblematic groups of the Cenozoic of this continent because of their great taxonomic diversity, abundant fossil record, and endemism (Gaudin and Croft 2015). During the Pleistocene of RS, xenarthrans were represented by two groups: pilosans (ground sloths) and cingulates (glyptodonts, armadillos, and pampatheres). Both megatheriid and mylodontid ground sloths have been found in RS Pleistocene deposits (Oliveira 1992, 1996). Megatheriid

Fig. 3.4 Late Pleistocene landscape of Rio Grande do Sul, showing from left to right the glyptodont *Glyptodon clavipes*, the ursid *Arctotherium*, the toxodontid *Toxodon platensis* (behind), and the megatheriid *Megatherium americanum.* The predominance of herbaceous vegetation is also evident, typical of parts of the landscape with a less significant presence of Araucaria Forest. (Artwork Julio Lacerda)

records include the co-occurrence of *Megatherium americanum* and *Eremotherium laurillardi* in at least two localities: Arroio Seival, Caçapava do Sul (Oliveira et al. 2002) and Chui Creek, Santa Vitória do Palmar (Lopes et al. 2019). This is the only Brazilian territory with records of both megatheriids, because *M. americanum* had an austral distribution and *E. laurillardi* had an intertropical distribution. Hence, RS was possibly a geographic boundary in the distribution of both species. The large mylodontid *Lestodon armatus* was reported from Caçapava do Sul and Chuí Creek (Vargas-Peixoto et al. 2021). Other ground sloths from the coastal plain of RS (CPRS) include the mylodontids *Mylodon darwinii*, the only record of this species in Brazil, *Glossotherium robustum*, and the scelidotheriine mylodontid *Catonyx* cf. *C. cuvieri* (Oliveira 1992; Lopes and Pereira 2010; Pitana et al. 2013). In western RS (WRS), ground sloths are rarer than in CPRS. Only records of the mylodontid *Glossotherium robustum* have been confidently reported (Pitana et al. 2013). Cingulates, especially glyptodonts, are common in RS Pleistocene deposits. However, most records are based on isolated osteoderms. The glyptodonts *Glyptodon clavipes* and *Panochthus* are present in most fossiliferous assemblages (Kerber and Oliveira 2008a; Pereira et al. 2012; Kerber et al. 2014a, b). Recently, large portions of carapaces, probably of *G. clavipes*, were found in the Ibicuí River, Alegrete, and Jaguarão, but the material is still undescribed (LK, pers. obs.). *Panochthus* from CPRS is represented by two species: *P. tuberculatus* and *Panochthus* cf. *P. greslebini* (Ferreira et al. 2015). *Doedicurus* is present only in deposits of the CPRS (Pereira et al. 2012), and rare material of *Neuryurus* was recorded from Garupá Creek, Quaraí (Kerber and Oliveira 2008b). The record of the enigmatic cingulate *Pachyarmatherium* is only based on isolated osteoderms from Balneário Hermenegildo (Lopes and Buchmann 2010). The pampatheres *Pampatherium humboldti* and *Holmesina paulacoutoi* have been documented from several Pleistocene deposits (Oliveira and Pereira 2009; Ferreira et al. 2018), although the species of *Pampatherium* of WRS is unknown (Kerber et al. 2014a, b). Dasypodids are the rarest cingulates, probably because of their smaller size, which makes it difficult to find their fossils. *Propraopus grandis* fossils have been mentioned for several localities (Pitana and Ribeiro 2007) and *Dasypus* sp. for the Chuí Creek (Oliveira and Pereira 2009).

Other iconic Cenozoic South American mammals are the native ungulates (Croft et al. 2020). These animals, possibly related to perissodactyls (horses, tapirs, rhinos, etc.; Laurasiatheria) (Buckley 2015; Croft et al. 2020), have five major lineages. The native ungulates from the Pleistocene of RS belong to two groups: notoungulates (toxodontids) and litopterns (protherotheriids and macraucheniids). Toxodontids are large herbivores, hippo-like mammals, and are represented by *Toxodon platensis* found in most Pleistocene localities of RS (Pereira et al. 2012; Kerber et al. 2014a, b). Proterotheriids are litopterns with more plesiomorphic morphological traits and are smaller than macraucheniids, which are characterized by elongated necks and nasal retraction. Fossils of the proterotheriid cf. *Neolicaphrium recens*, the only Quaternary survivor of the lineage (Bond et al. 2001), were found in the Hermenegildo Beach (Santa Vitória do Palmar) (Scherer et al. 2009). Like

T. platensis, the macraucheniid *Macrauchenia patachonica* has also been found in several localities (Scherer et al. 2009).

Euarchontoglires is represented by rodents. Two groups are found in Pleistocene sediments of RS: caviomorphs (African origin) and cricetids (Holartic origin). Together, both lineages compose the most diversified lineage of South American mammals (D'Elía et al. 2019). The Pleistocene record of caviomorphs includes the capybara (*Hydrochoerus hydrochaeris*) and the coypu (*Myocastor coypus*) in deposits from WRS and CPRS (Kerber and Ribeiro 2011; Kerber et al. 2014a, b). A fossil of the cavy *Galea* sp. (absent in the RS modern mastofauna) was found in deposits of the Touro Passo Creek (Kerber et al. 2011b). Similarly, in the fossiliferous assemblage from the Chuí Creek, three rodents that currently inhabit drier areas of southern South America have been found: the cavy *Microcavia*, the vizcacha *Lagostomus* cf. *maximus*, and the mara Dolichotinae indet. (Ubilla et al. 2008; Kerber et al. 2011c). The fossil record of cricetids is scarce, represented by remains of *Reithrodon auritus* from Balneário Hermenegildo (Rodrigues and Ferigolo 2004) and *Holochilus brasiliensis* from WRS and CPRS (Kerber et al. 2012).

Like cricetids, other mammalian lineages recorded in Pleistocene deposits of RS have a Holarctic origin, and their ancestral lineages arrived during the Plio-Pleistocene GABI (see Woodburne 2010; Goin et al. 2012). Most of them had wide geographic distributions in the South American Pleistocene. Artiodactyla is the most diverse clade of laurasiatherians, with three groups: tayassuids, camelids, and cervids. Tayassuids (peccaries) show records of the extant white-lipped peccary *Tayassu pecari* at Touro Passo Creek, and of the large extinct *Brasiliochoerus stenocephalus* in WRS as well as in CPRS (Gasparini et al. 2009; Kerber et al. 2014a, b; Copetti et al. 2021). Camelids, the llamas and guanacos, are represented by three species in several localities: the extant guanaco *Lama guanicoe* and the vicuña *L.* aff. *gracilis*, and extinct *Hemiauchenia paradoxa* (Scherer 2006; Scherer et al. 2007). Cervids (deers) have records of indeterminate species of the extant genus *Mazama* in the CPRS, and the extinct genus *Morenelaphus*, and the large *Antifer* in several localities (Kerber et al. 2014a, b; Pereira et al. 2012; Fontoura et al. 2020).

Perissodactyls include two species of horses, *Equus neogeus* and *Hippidion principale*, and the tapir *Tapirus* cf. *terrestris*, which were widely distributed (Pereira et al. 2012; Holanda et al. 2012; Kerber et al. 2014a, b). The fossil record of carnivorans is rare, and most fossils come from the CPRS. Few specimens of the canid *Dusicyon* cf. *D. avus*, and the large hypercarnivore forms *Protocyon troglodytes* and cf. *Theriodictis* are recorded from the CPRS, as well as the iconic saber-toothed cat *Smilodon popularis* and the jaguar *Panthera onca* (Rodrigues et al. 2004; Lopes et al. 2020). Ursids are known from undescribed bones from Quaraí River, an isolated tooth from Pantano Grande, and a canine assigned to cf. *Arctotherium* from Chuí Creek (Pereira et al. 2012). Afrotherians are represented by proboscids, with records of mastodont *Notiomastodon platensis* from several localities (Marcon 2008).

Other continental tetrapods are much less abundant and studied. From the Touro Passo Creek, there are some records of chelonians, not described in detail, such as *Hydromedusa tectifera* (Maciel et al. 1996; Hsiou 2009), the endemic extinct teiid lizard *Tupinambis uruguaianensis* (Hsiou 2007), and the tropical stork *Mycteria* cf. *M. americana* (Ribeiro et al. 1995; Hsiou 2009). Finally, the tropical stork *Ciconia* is recorded from Chuí Creek (Lopes et al. 2019).

Due to the geographic location of RS, the Pleistocene fossils are in the geographic boundary between two biogeographic regions, the Pampean and Intertropical regions (Oliveira 1999; Oliveira et al. 2002; Oliveira and Pereira 2009; Kerber et al. 2014a, b; Lopes et al. 2019, 2020). For this reason, their taxonomic composition show a mix of taxa predominantly recorded in the southernmost parts of South America (e.g., *Doedicurus* and *Macrauchenia*) and forms of intertropical affinities (e.g., *Eremotherium*). Most large mammals were extinct at the end of the Pleistocene and early Holocene. During the Holocene, the taxonomic composition of the modern faunas originated (see Hadler et al. 2008, 2009, 2016; Lopes et al. 2020 and references therein for a review). Although the causes of this extinction event of continental proportions are still debated, it is inferred that the extinctions were not simultaneous, but occurred over the course of a few thousand years. (Lopes et al. 2020). According to the model proposed by Lopes et al. (2020), the most recent study on RS extinctions, large mammals disappeared in at least two phases, which can be related to climatic changes in the Late Pleistocene. The first phase occurred around 30 ka in the CPRS, predating the arrival of humans into the region by about 25 ka. A second phase eliminated taxa that survived until about 12.7 ka in reduced suitable environments associated with perennial rivers of the WRS. This phase coincides with the transition from glacial to interglacial conditions. Finally, it was suggested that early human occupations may have contributed to environmental modifications. No confident archaeological records of humans' coexistence or exploitation of extinct mammals have been documented in RS yet, although there are plenty of them in South America (Bampi et al. 2022). However, early inhabitants may have contributed to environmental changes through the use of fire for agricultural purposes (Behling et al. 2009).

It is clear that it was the climatic variation over time that outlined the environmental mosaic of the *Campos Sulinos* region. Different studies confirm that grassland vegetation is much older than forests in the Pleistocene phytogeography of southern Brazil. During much of the Pleistocene, the landscape that made up these environments was predominantly grassland vegetation, with rivers not accompanied by riparian forests. These open areas were populated by megafauna and had a humid and cold climate for most of the year (Scherer and Da Rosa 2003; Behling et al. 2009). The presence of megafauna also played an important role in vegetation dynamics, and herbivory action guided the process of plant evolution and their morphological patterns. Studies carried out in savannah areas of South America and Africa show that the vegetation coexisting with the past megafauna developed specific protection mechanisms, such as thorns and smaller and rigid leaves, including the production of unpalatable chemical substances to minimize predation (Dantas and Pausas 2022). Thus, large herbivorous mammals also maintained grassland vegetation for a long time during the Pleistocene. After the extinction of the megafauna, an opportunity for the expansion of forest was created (Behling et al. 2009; Dantas and Pausas 2022). The development of vegetation cover in southern Brazil can be traced from the palynological record of peats recovered in different locations in the southern states of Brazil: Paraná (Behling 1997), Santa Catarina (Behling 1995), and Rio Grande do Sul (Roth and Lorscheitter 1993; Behling et al. 2001, 2004), which abundantly preserve pollen from the Pleistocene, including species of Poaceae, Cyperaceae, and Asteraceae, all typical of grassland communities. On the other hand, the presence of forests in the region, especially the Araucaria Forest, and their expansion over grasslands vegetation is only verified from 3 ka AP on, associated with the increase and frequency of rainfall. At first, forests were restricted to areas close to water bodies; later, they advanced over grassland vegetation in areas farther away (Behling et al. 2009). In addition, the presence of charcoal in palynological slides (e.g., Behling et al. 1995, 2005; Ribeiro et al. 2020) is evidence of paleowildfires during the Pleistocene in the *Campos Sulinos* (Behling et al. 2009). Fire is one of the key modeling elements of past ecosystems (e.g., Scott and Stea 2002; Scott and Damblon 2010; Manfroi et al. 2023), and can be compared to herbivory as a modifier of different biomes over time (Bond and Keeley 2005). In the *Campos Sulinos*, we thus conclude that both fire and herbivory were instrumental in restricting forest expansion over grasslands during much of the Pleistocene (see also Behling et al. 2023, Chap. 4, in this volume).

3.4 Summary and Conclusions

3.4.1 Earlier Ecosystems

Permian ecosystems are directly related to Pangean conditions, ranging from glacial to desert environments, including epicontinental marine forms. In these scenarios, the fossils from early Permian (Sakmarian-Artinskian) of southern Brazil record several ecosystems, from glacial and postglacial highlands and lowlands covered with shrubs and forests, to coastal lagoons and sandy barriers coupled with peat environments, and recurrent wildfires. Middle Permian deposits only record an epicontinental sea and its coastal environments, but no continental succession is known so far. The late Permian sediments record the continentalization of Gondwana, and the formation of complex food chains of amniotes and temnospondyls in flat alluvial plains covered with shrubs and small forests, also subject to wildfires.

Triassic ecosystems also relate to Pangean conditions, but resulted from environmental and biotic recovery after the most massive extinction event, and later the continental breakup forming Laurasia and Gondwana. The early Triassic deposits (Olenekian) gave rise to alluvial plain ecosystems, with fish, temnospondyls, and archosauriforms, in a food chain not yet detailed. Middle and Late Triassic deposits can be related to two different fluvial scenarios: low energy, high sinuosity rivers, and related floodplain environments (Ladinian and Carnian), and high energy rivers with restricted overbank deposits (Norian). There is a dominance of archosaurs and synapsids (cynodonts and dicynodonts) at first, in *Dinodontosaurus* and

Santacruzodon Assemblage Zones (AZ's), followed by the disappearance of dicynodonts or their substitution by specialized herbivores and the irradiation of more agile carnivores, respectively, rhynchosaurs and dinosaurs, in *Hyperodapedon* AZ. The *Riograndia* AZ records the return of dicynodonts, but in ecosystems mainly occupied by cynodonts and sauropodomorph dinosaurs as main herbivores, and a plethora of carnivores, such as cynodonts, dinosaurs, and archosaurs. The twofold scenario is also recorded by the presence of shrubby plants of the *Dicroidium* Flora that are later replaced by the Conifer Flora, more related to forests.

Late Jurassic land faunas are known only by their ichnological remains, found in association with typically aeolian deposits, a result of arid desertic environments. Despite that, the yet poorly known fossil record of this timespan reveals the presence of an association of medium to large-sized herbivore and carnivore dinosaurs. More data on southern Brazil Jurassic faunas are needed in order to better understand the ecological dynamics of ecosystems.

3.4.2 Pleistocene and Modern Ecosystems

The present relief of southern Brazil is a post-Cretaceous construction that formed after the breakup of South America and Africa. Most rivers started flowing inward and later toward the Atlantic Ocean, forming the coastal plain and continental platform (Potter 1997). The result of fluvial erosion is recorded in the Pelotas Basin's Cretaceous, Paleogene, and Neogene succession (Anjos-Zerfass et al. 2008).

Along the last 400 ka, the intercalation of glacial and interglacial cycles led to the formation of a mosaic of forests and grasslands, each cycle favoring a specific environment and associated flora and fauna. The onset of interglacial cycles led to sea level rise, and the continental onward shift of the coastline, preserving lagoons and sandy barriers at the coastal plain of Rio Grande do Sul. In contrast, the glacial cycles shifted the same coastline basinward, i.e., at least 100 km from the present shoreline, depositing fluvial sediments along the submerged continental platform (Lopes et al. 2021). On the continental side, the glacial cycles reinforced fluvial erosion, due to river profile lowering. In contrast, the interglacial cycles favored fluvial deposition, through progressive drowning of the river profile (see references in Maahs et al. 2019).

Some ecological processes are considered important in shaping the *Campos Sulinos* landscapes, both in the past and today. The action of fire on vegetation, for example, is recognized as an important controller in the maintenance of ecosystems, and evidence of fire exist especially in the more recent past (the last 600 years), despite humid climatic conditions during this period. Likely, occurrence of fire is related to human populations, did not allow for widespread development of forests and keeping grassland vegetation as the predominant system (e.g., Behling et al. 2009; Piperno and Becker 1996; see also Behling et al. 2023, Chap. 4 in this volume). Along with fire, the influence of herbivore animals is likely equally important in the dynamics of the *Campos Sulinos* landscapes. Whether large herbivore mammals that inhabited the region until 8500 years ago (Scherer and Da Rosa 2003) or cattle introduced by the Jesuits in the seventeenth century (Porto 1954), herbivores consume plants and prevent the expansion of woody vegetation, while also limiting the accumulation of biomass and thus preventing the availability of fuel for larger fires (Behling et al. 2009). Clearly, human occupation has had an influence on natural environments from their earliest beginnings.

The fossil record of the region known today as the *Campos Sulinos* is extremely rich and dates back to 300 million years ago. These fossils testify important paleogeographic, paleoclimatic, and paleofaunistic shifts, and provide evidence for the origin and evolution of the different ecosystems. It is impossible to study the region's biodiversity without considering its past, including biotic and abiotic events that occurred during the Cenozoic and probably acted as shaping agents of environments and current biodiversity.

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Chapter 4
Dynamics of South Brazilian Grasslands During the Late Quaternary

Hermann Behling, Valério D. Pillar, and Gerhard Ernst Overbeck

4.1 Introduction

Subtropical grasslands in Brazil present high biodiversity and are the predominant vegetation type in the south of the country (e.g., Andrade et al. 2019; Overbeck et al. 2022). The analysis of spatial and temporal variation in tropical and subtropical grassy biomes, such as shifts in the limits between forests and grasslands and floristic changes in grassland vegetation over the past millennia, contribute to the understanding of current biodiversity patterns of South Brazilian grasslands. However, the history of the South Brazilian grasslands, and with it the history of fire and human impacts, has only relatively recently been subject of scientific studies.[1]

Today, landscapes characterized by grasslands and forest-grassland mosaics that still preserve their natural aspect can still be found over considerable extent (Fig. 4.1), despite the massive recent landscape changes caused by agriculture and silviculture. An important question is whether these grasslands are natural or shaped by pre- and post-Columbian human intervention. Forest-grassland mosaics have instigated naturalists and ecologists for a very long time. Past researchers, such as

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[1] This contribution follows, in part and with adaptations, a previous synthesis of the Late Quaternary vegetation history of southern Brazil that was only available in Portuguese (Behling et al. 2009).

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Fig. 4.1 Mosaics of *Araucaria* forest and grassland on the South Brazilian highland. (Photo V. Pillar)

Lindman – who traveled through southern Brazil in the late nineteenth century – noticed that the forest vegetation should be able to expand over grasslands, attributing the existence of the mosaic to the transitional region between the forest vegetation from the north and the grasslands in the south (Lindman 1906). Based on phytogeographical evidence, Rambo (1956a, b) and Klein (1975) deduced that grasslands were the more ancient vegetation type, while forests were newer, arising from climate shifting toward more humid conditions. Hueck (1966) also questioned the existence of grasslands in southern Brazil under current humid climatic conditions that are suitable for forest vegetation.

Knowledge about the origin of grasslands is paramount for their conservation. If, on the one hand, forest-grassland mosaics were the consequence of human activities caused by deforestation and the use of fire, conservation strategies, including vegetation management, should focus on recovery of the forest vegetation. However, if, on the other hand, grasslands were pristine and persisted under different climate regimes, they should be highly valued for being natural relics with high biodiversity, and the management practices that maintain them should be valued and supported. Prehistoric and historic knowledge about fire frequency and intensity and their effects on vegetation could be used in creating long-term sustainable management plans and monitoring. Questions in this context are whether fires were (or are) natural and anthropogenic? Do human impacts differ between pre- and post-Colombian times? What would be the effect of large grazers, extinct thousands of years ago, on current grassland species evolution? What was the effect of past climate changes on these forest-grassland mosaics? How should we manage and conserve these mosaics with forests and grasslands that are both species rich ecosystems?

With the help of a synthesis of paleoecological studies from southern Brazil, conducted over the past 25 years, the objective of this chapter is to demonstrate the importance of knowing past vegetation and environmental dynamics for a holistic understanding of grassland ecosystems. Such information is crucial and should be considered, together with other data, when planning grassland conservation, restoration, and management strategies.

4.2 The South Brazilian Grassland Region

The South Brazilian grassland region comprises grassland areas in the states of Rio Grande do Sul, Santa Catarina, and Paraná. The region's landscape is characterized by the Coastal Plain along the Atlantic coast, the Central Depression, the *Campanha* region, the Southeastern Highlands, and the Southern Brazilian Plateau (between 500 and 1200 m), to cite only the main major geomorphological units. Above 1200 m, the plateau is formed by the *Serra Geral* that extends toward the south and continues northeast through the *Serra do Mar* mountain range (see also Menegat 2023, Chap. 2, and Hasenack et al. 2023, Chap. 6, this volume).

The region's climate is controlled by the South Atlantic anticyclone, a semipermanent high-pressure system that carries humid tropical air masses from the ocean toward the continent, from east to west, all year round (see Hasenack et al. 2023, Chap. 6, this volume). Additionally, in southern Brazil, the annual variation in the Intertropical Convergence Zone (ITCZ) causes abundant precipitation during the summer months (October–March) and less rainfall from April to September, leading to not so wet periods. The clash between Antarctic polar cold fronts and the tropical air masses can result in heavy rains. This phenomenon is especially present in southern Brazil, resulting in a short or absent dry season (Nimer 1989; Hastenrath 1991). Recently, several longer drought events over summer have occurred, which may increase the frequency of fire (e.g., Pivello et al. 2021).

The current potential natural vegetation in southern Brazil includes forest ecosystems – Tropical Rainforest (Atlantic Forest *sensus stricto*), *Araucaria* Forest, and Semi-Deciduous Forests (e.g., Oliveira-Filho et al. 2015) – and grasslands (Overbeck et al. 2022). The frost-sensitive Atlantic Forest reaches its southern limit in the region, extending like a belt along the Atlantic coast and over the *Serra Geral* and *Serra do Mar* eastern cliffs (Klein 1978; Por 1992). The annual mean temperature is between 17° and 24 °C with year-round rainfall. The *Araucaria* Forest can be found in higher areas, between 24° and 30°S latitudes, mainly between 1000 and 1400 m elevation (Hueck 1966), in mosaics with grassland. The annual mean temperature is between 12° and 18 °C, but cold nights can reach from −4° to −8 °C in the higher portions of *Serra Geral* (Nimer 1989). Current grassland ecosystems in southern Brazil include the grasslands in the Pampa and the High Elevation Grasslands (*Campos de Altitude*). In general, the forest cover in the region increases from south to north. The Pampa grasslands are found in the Central Depression, the Southeastern Highlands, and the *Campanha* regions, all in the southern portion of Rio Grande do Sul. The vegetation here is similar to the Uruguayan and Argentine grasslands; indeed, together with these regions the Pampa grasslands form the region of the '*Pastizales del Río de la Plata*' (Andrade et al. 2019).

Grasslands (*Campos*) are frequently divided into "*campo limpo*", dominated by grasses and sedges, along with many other herbs and small shrubs from different botanical families, and "*campo sujo*", where shrubs, especially from the Asteraceae family (*Baccharis dracunculifolia, B. uncinella,* among others), and some other taller plants, such as *Eryngium* spp. (Apiaceae) can be found along with grasses and short herbs (Klein 1978; Andrade et al. 2019). Both types of *campo* hold a high number of herbaceous species (Rambo 1956b; Klein 1979; da Silva Menezes et al. 2018). The *Campos de Altitude* also occur at the peaks in the mountain ranges along the Brazilian Atlantic Coast in southern and southeastern Brazil (above 1600 m and 1800 m elevation, respectively). In these locations, shrub species, belonging, for example, to the Melastomataceae, Ericaceae, Eriocaulaceae, Asteraceae, and Verbenaceae families are important elements of the vegetation (Safford 1999a, b). These grasslands also hold several endemic species (Ferrão and Soares 1989; see also Overbeck et al. 2022).

4.3 Reconstruction of Past Vegetation and Environments

The palynological analysis of peat bogs, lakes, or other organic sediment deposits is an important tool for reconstruction of the vegetation and environmental history of a given region (Fig. 4.2). Because pollen is preserved under the anoxic conditions of these organic deposits, they become archival sedimentological samples, representing the past vegetation. In other words, we can reconstruct the region's paleovegetation and paleoenvironment based on the analyses and interpretation of pollen records (Fig. 4.3).

The South Brazilian highland region is especially interesting in this regard due to the presence of peat bogs. Poaceae, Cyperaceae, and other typical grassland pollen allow the identification of the grassland communities to which they used to belong. For the construction of a paleovegetation, the specific site conditions and the proportion of pollen from the local vegetation, including peat bogs or the lake margins, depending on each case, should also be considered. Novel techniques for studying Poaceae pollen morphology can provide information on grass development, dynamics, and diversity (Schüler and Behling 2011a, b). Additionally, the abundance of charcoal particles in the sediment profile delivers data on the frequency and intensity of fires. Furthermore, organic sediment radiocarbon dating offers chronological control of past environmental changes. Pollen and charcoal data are then illustrated as diagrams used as the basis for the reconstruction of the past vegetation (Fig. 4.4a, b). In the following, we present results from several sites in southern Brazil that generate a rather detailed knowledge of the vegetation and the environmental changes that occurred in the past 40,000 years during the Late Quaternary (Late Pleistocene and Holocene).

Fig. 4.2 An intact peatbog in the South Brazilian highland. (Photo V. Pillar)

Fig. 4.3 Collection of a sediment core from a peat bog in southern Brazil. (Photo V. Pillar)

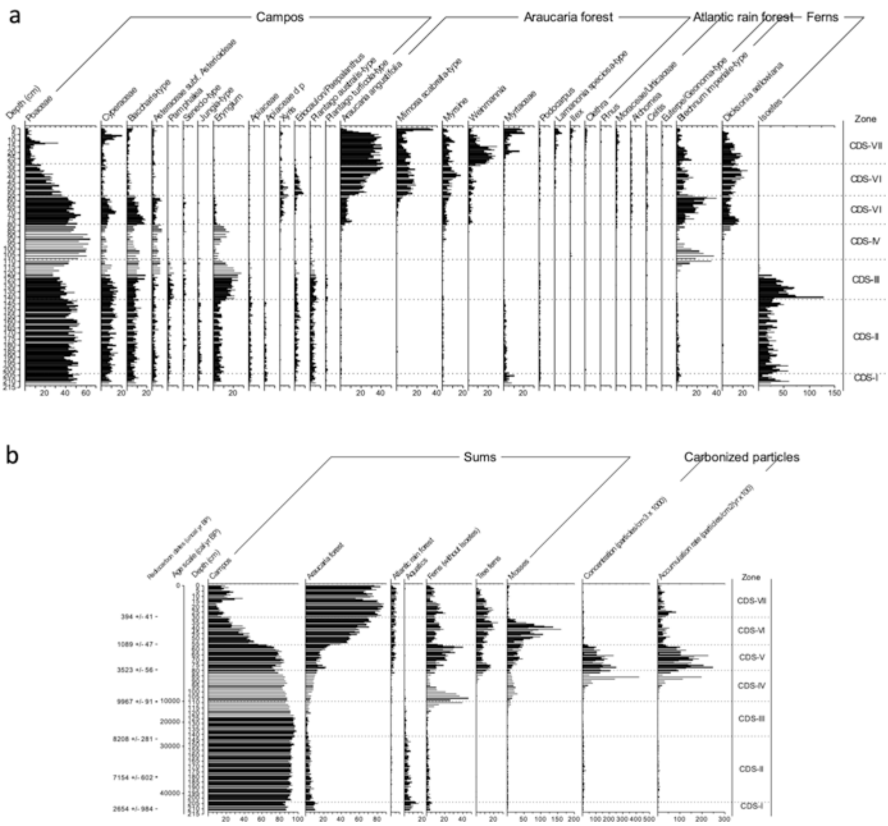

Fig. 4.4 Percentage (**a**) and summary (**b**) pollen diagram for Cambará do Sul, including the radiocarbon dates, age scale (cal yr BP), records of different taxa and ecological groups (*Campos*, *Araucaria* forest, Atlantic rainforest, Ferns), concentration and influx of carbonized particles, and pollen zones. (For more details see Behling et al. (2004))

4.4 The History of the Southern Brazilian Grasslands During the Late Quaternary

4.4.1 Paleoenvironmental and Paleovegetational Changes

Several palynological studies have been conducted in southern Brazil over the last decades. Data from Paraná (Serra dos Campos Gerais: Behling 1997), Santa Catarina (Serra do Rio do Rastro, Morro da Igreja, Serra da Boa Vista: Behling 1995), and Rio Grande do Sul (Aparados da Serra: Roth and Lorscheitter (1993); São Francisco de Paula: Behling et al. (2001); Cambará do Sul: Behling et al. (2004)), i.e., from the South Brazilian Highland region, have proven the existence of large grassland areas on the Plateau during the glacial times and the early and mid-Holocene. The dominance of grasslands is attributed to the cold and dry glacial climate and the warm and dry early Holocene climate. The early and mid-Holocene were characterized by a long annual dry season of around three months (Behling 1997, 2002).

The expansion of the *Araucaria* Forest over grasslands started on the Plateau around 3210 years cal BP (calibrated age in radiocarbon years before present; actually, the year 1950 is the reference for "present" in radiocarbon dating). The expansion began with the migration of gallery forests along rivers, which indicates the change to wetter climatic conditions without a reduction of the dry season. This process seems to have accelerated circa 1400 years cal BP in Paraná and 930 years cal BP in Santa Catarina. A peat bog sedimentary profile located 7 km from Cambará do Sul in Rio Grande do Sul (RS) State allowed us to produce a detailed pollen diagram that reached 42,840 years ^{14}C BP (noncalibrated age in radiocarbon years before present) (Fig. 4.4a, b). From that, Behling et al. (2004) published a complete paleoenvironmental and paleovegetational description, including selected records of pollen and spores. The Cambará do Sul's record documents the grassland vegetation dynamic followed by *Araucaria* Forest expansion. Trees were likely absent from the plateau region, northeastern RS, between 42,840 years ^{14}C BP and 11,500 years cal BP (Late Pleistocene). The few pollen grains representative of the *Araucaria* Forest vegetation found in the Late Pleistocene sediment could be associated with wind dispersal. They were likely transported from forest refuges protected deep in the valleys from the plateau or the Serra Geral cliffs, distant 6 to 7 km, or even from the coastal mountains.

The vast grassland vegetation indicates cold and dry climatic conditions in the Late Pleistocene. The data suggest that the winter months had frequent and minimum temperatures reaching −10 °C. Between 26,000 and 17,000 years ^{14}C BP, during the Last Glacial Maximum (LGM), the mean annual temperature was probably around 5° to 7 °C colder than present conditions (Behling and Lichte 1997). *Eryngium* sp. pollen was abundantly found in the LGM sediment, indicating drier climatic conditions. Around the same period, peat bogs used to be shallow intermittent lakes, meaning seasonal droughts. Records from Cambará do Sul suggest that the seasonality increased after 26,900 years ^{14}C BP. The prevalent climate was seasonal, with a long annual dry period from the LGM to the early Holocene.

A different palynological sample from *Volta Velha Preserve*, located within the Atlantic Forest domain between Santa Catarina and Paraná, dated 26,000 years, points to forest and grassland species adapted to the cold during the entire glacial period (Behling and Negrelle 2001). Grasslands were abundant in the coastal region and over the continental shield, while the tropical tree species (i.e., *Alchornea* sp. and palms) were largely absent, especially during the LGM. The tropical vegetation was replaced by grasslands and cold-adapted forests, pushing it to migrate around 500 km north, indicating that the climate was 3 to 7 degrees cooler during the LGM (Behling and Negrelle 2001). After that, the tropical forest (Atlantic Forest) replaced the cold-adapted grassland communities.

Grasslands remained dominant on the plateau during the early and mid-Holocene (11,500 to 4320 years cal BP). There was a slight increase in *Araucaria* Forest species, but they were still sparse, suggesting they migrated to the study area (Cambará do Sul) through narrow corridors. Pollen grains from Atlantic Forest taxa increase in frequency, suggesting this vegetation expanded over the nearby *Serra Geral* slopes. Extensive grassland areas coupled with rare *Araucaria* Forest taxa indicate a dry climate, while floristic changes in grasslands' species composition point to a shift to a warmer and drier climate. Annual precipitation was likely below 1400 mm, and the dry season was probably three months long, meaning that the climate conditions were unfavorable to the Araucaria Forest expansion in this area during the early and mid-Holocene.

Only during the late Holocene did the Araucaria Forest expand around Cambará do Sul, forming a network of gallery forests, although grasslands were still regionally dominant. The *Araucaria* Forest included populations of *Myrsine* sp., and more sparsely, *Mimosa scabrella*, Myrtaceae species, *Podocarpus* sp., and *Ilex* sp. Tree ferns (*Dicksonia sellowiana*) were already common in the gallery forests. During the late Holocene, the Atlantic Forest and likely the Cloud Forest were well established in the Plateau cliffs, located around 6–10 km from the studied area.

Results from Cambará do Sul indicate that the original grasslands were replaced entirely by forest in the surroundings of the sampled area (Table 4.1). However, other pollen records, e.g., from the *Serra dos Campos Gerais*, document the development of grassland-forest mosaics during the late Holocene.

Other studies were conducted in the *Campanha* region near São Francisco de Assis, in western Rio Grande do Sul (Behling et al. 2005). The area was naturally covered with grasslands during the glaciation and the Holocene under cold and relatively dry conditions. The initial expansion of gallery forests, after 5170 years cal BP, occurred with the shift to more humid conditions. The peak of forest expansion, around 1550 years cal BP, corresponds to the most humid period on record;

Table 4.1 Summary of key results from paleoecological studies conducted in southern Brazil

Geological Period		Vegetation	Climate
Last Glacial Maximum	~18 ka BP	Predominantly grasslands	Markedly dry and 5–7 °C below current temperature
Late Glacial	14–10 ka BP	Predominantly grasslands	Still very dry and cold
Early Holocene	10–7.5 ka BP	Predominantly grasslands	Dry and cold climate with dry periods of ~3 months per year
Mid--Holocene	7.5–4 ka BP	Still predominantly grasslands	Lower Holocene climate conditions still predominate
Late Holocene	4 ka BP – present	From 3 ka BP: *Araucaria* Forest starts to expand over grasslands through refuges in higher areas along rivers Only after 1 to 1.5 ka BP: Beginning of widespread *Araucaria* Forest expansion, replacing grasslands in high areas as well	Increase in precipitation frequency and amount Current humid climate conditions, with or without a short dry period

See text for details

however, the region primarily remained as grasslands until now. A study conducted in Caçapava do Sul, situated in the low *Serra do Sudeste* mountain range in the southern half of Rio Grande do Sul state, within the Pampa biome, covers a period of just over 500 years. The region's conditions are not very suitable for the formation of swamps or beat bogs. Although the results from this site (Behling et al. 2016) are somewhat limited, they bring interesting findings. The study reveals that populations of *Araucaria angustifolia*, along with other forest species associated with it, existed in this region before European colonization. Furthermore, the study provides evidence of the presence of forests in the region in the recent past, which continues to be the case today, as large portions of area are covered by forest--grassland mosaics.

4.4.2 The Influence of Grazers

By the time cattle were introduced in the region by the Jesuits in the seventeenth century, the local grazing fauna was composed of small-sized animals such as deer, emu, capybaras, tapir, and small rodents. These species exerted a localized grazing pressure, unlikely to control the woody vegetation expansion. Fossil records show, however, evidence of large grazer species related to horses (Equidae) and llamas (Camelidae), as well as other large herbivores that inhabited the region until 8500 years ago (Kern 1997; Scherer and Da Rosa 2003; Scherer et al. 2007; Prates and Perez 2021; Paruelo et al. 2022; see also Da Rosa et al. 2023, Chap. 3, this volume).

The impact of those large grazers on the dynamics of native grasslands is still to be determined. Nevertheless, since the collision of South and North Americas during the Upper Pliocene, around 3 million years ago, the vegetation must have endured the combined effects of the local fauna and the invasion by large North American ungulates that had grazing patterns similar to the later introduced cattle (Schüle 1990). Grazing by large herbivores is not far from the current grasslands' flora evolution, as evidenced in the fossil record. We can, thus, hypothesize that the lack of grazers during these 8000 years between their extinction and the cattle introduction must have influenced the increase of grassland fires in that period.

4.4.3 Fire Frequency and Forest Expansion

Results from pollen samples collected between Cambará do Sul and São José dos Ausentes point to a strong association between the *Araucaria* Forest expansion and fire frequency in the last 600 years (Jeske-Pieruschka et al. 2010). Grasslands surrounded the studied peat bog and also bordered a small *Araucaria* Forest patch, offering the ideal conditions to investigate its origin, dynamics, and stability, including the influence of possible anthropic activities. The sample, 120-cm long and dated 590 years cal BP, reveals clear changes in local vegetation during the last centuries. According to the pollen data, the area was dominated by grasslands. The *Araucaria* Forest patch was absent or very small between 590 and 540 years cal BP (1360 to 1410 *Anno Domini* (AD)). The frequent fires, usual during this period, possibly hindered forest development, despite the very humid climate conditions. The establishment or expansion of forests happened around 540 and 450 years cal BP (1400 to 1500 AD), mainly through pioneer taxa such as *Myrsine*, *Ilex*, Melastomataceae, and a few Myrtaceae. The phenomenon was presumably linked to less frequent fires, as deduced from the charcoal particles in the palynological profile. From around 450 to 370 years cal BP (1500 até 1580 AD), the grassland-covered areas increased while the *Araucaria* Forest stopped expanding and shrunk. Large amounts of charred particles were found during this period, pointing to fire as the primary driver of vegetational changes. From around 370 to 15 years cal BP (1580 to 1935), the *Araucaria* Forest resumed its expansion after fire frequency decreased. Recently, 15 years cal BP (1935 AD) to the present, the vegetation composition underwent significant changes. First, the grassland area markedly reduced while the forest patch close to the peat bog kept expanding. A few tree species, typical of secondary vegetation, are more frequently found, which can be linked to recent forest degradation likely caused by selective logging and cattle inside the forest. The apparent expansion of the small *Araucaria* Forest patch within the last 70 years is clearly associated with the sharp decrease in fire frequency. Fire frequency is a key factor regulating the dynamics and stability of *Araucaria* Forest-grassland mosaics (Sühs et al. 2021).

At the Morro Santana, in Porto Alegre, one of the granitic hills that forms the northeastern portion of the *Serra do Sudeste* Highlands, palynological and charcoal analyses revealed that the vegetation used to be a high diversity forest-grassland mosaic under the influence of fire during the late Holocene. Grassland taxa were well represented between 1230 and 580 years cal BP, while forest taxa were less abundant. The grassland vegetation was composed of Poaceae, Cyperaceae, and Asteraceae; the most important genera were *Eryngium* and *Eriocaulon*. Some of the Cyperaceae pollen could be from the studied bog itself. Forest taxa such as Moraceae/Urticaceae or Myrtaceae were rare. After 580 years cal BP, *Baccharis* sp. increased, while *Eryngium* sp. decreased, among others, indicating changes in the floristic composition of grasslands, which later reappeared between 380 and 300 years cal BP. This trend can be interpreted as an indicator for decline in fire frequency. *Baccharis* is the most important shrub genus in present-day grasslands in the region, and population development of many woody species is associated to longer periods without fire periods (Müller et al. 2007), as indicated by a negative correlation of these species to charcoal concentration. On the other hand, *Eryngium*, which was positively correlated with charcoal concentration, is a genus specialized in disturbances, thriving in the presence of fires (i.e., presenting higher abundance and reproduction rates) (Fidelis et al. 2008). As typical grassland genus, *Eryngium* species are expected to drop in importance with longer fireless gaps or forest invasion. From the following period to the present, the forest continues to expand, as evidenced by the increase in *Myrsine*, a pioneer forest genus, negatively correlated to charcoal concentration, suggesting a possible change in the disturbance regime.

4.5 Ecological Study of Graminoids Based on Morphological Pollen Data

With new methods, it is possible to distinguish between different grassland types based on the morphology of the grass species pollen in organic deposits. For instance, Schüler & Behling (2011a, b) distinguish four main grassland vegetation types in South America based on their pollen: *Paramos* in Ecuador, *Pampas* in Argentina, *Campos* in southern Brazil, and *Campos de Altitude* in Southeastern Brazil, and even infer their diversity patterns. As shown in Fig. 4.5, grassland pollen grains from *Paramos* are larger than those the other grassland types that present similar sizes, and pollen size range appeared as an important feature to distinguish grassland types, as long as variations within each species are minor (Joly et al. 2007). The pilot study by Schüler and Behling (2011a, b) suggests that the taxonomic similarities between *Campos*, *Campos de Altitude*, and Pampa are much greater than the similarities between *Campos* and *Paramo*. Within the latter, pollen lengths' range indicates huge differences in taxonomic presence and dominance,

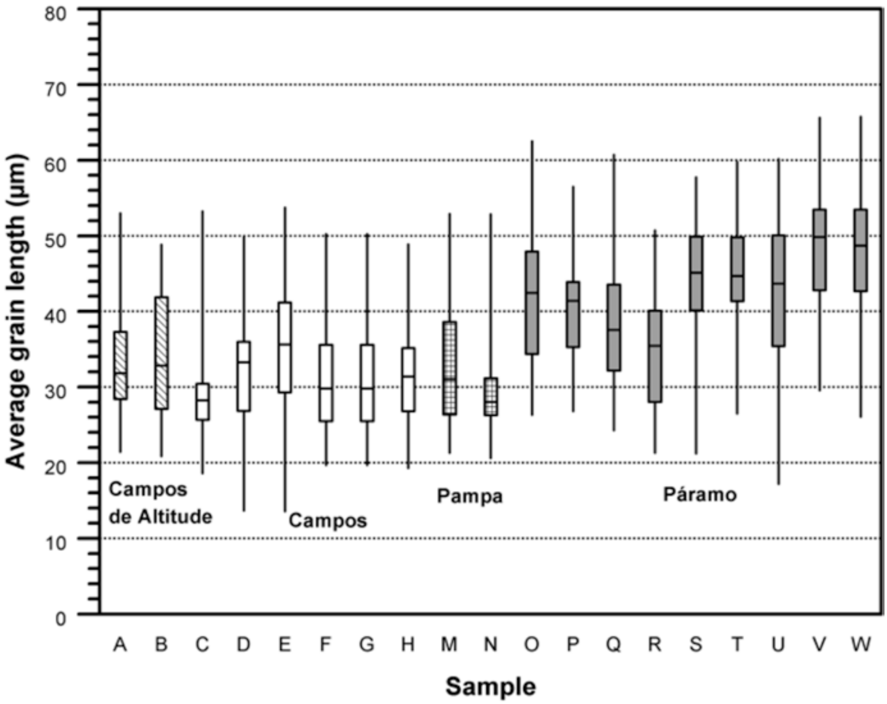

Fig. 4.5 Diagram showing differences in average pollen grain length between grassland vegetation types and variability within vegetation types. Each column represents a sample. The fill patterns in each column constitute 50% of all pollen grains measured within the same sample, where the vertical lines above and below each column represent 95% of all grains. The vertical black line in the center of each column marks the average grain length for that sample.

supporting that, when considering grasses composition, the South Brazilian *Campos*, including Pampa grasslands and highland grasslands in Southern Brazil, are more similar to geographically closer grassland ecosystems (*Campos de Altitude*) than to the northern Andes *Paramo* region (Safford 1999a, b). From pollen grains' length and taxonomic composition, it is also possible to deduce diversity changes through the temporal scale, and this worked especially well for South Brazilian grasslands. For instance, a taxon found in the early Holocene samples was absent from the late Pleistocene grasslands, implying that grassland diversity changes over time. This could have been caused by shifts toward more humid conditions during the late Holocene, with strong effects of regional biodiversity.

4.6 The History of Fire Dynamics and Human Impact in Southern Brazil

The role of fire, including its origin – whether naturally caused by lightning or by humans as a hunting artifact – and its effects on vegetation must be understood to be able to understand the ecology of South Brazilian grasslands, including for management-related questions, e.g., in conservation. South Brazilian sedimentological profiles that include data on charcoal particles are scarce. Data from the Campos Gerais region in Paraná state, i.e., the northern part of the Campos Sulinos, and from São Francisco de Assis in the Pampa region show that fire was rare during the glacial period and barely affected grasslands (Behling 1997; Behling et al. 2004), while a rise in fire frequency was observed from the beginning of the Holocene.

Records from the Cambará do Sul area, in the highland region of Rio Grande do Sul (Fig. 4.4a, b) confirm this trend, showing low amounts of charcoal particles, which indicate rare naturally originated fires during the glacial period (between 42,840 years ^{14}C BP and 11,500 years cal BP). The same profile shows that fires became more frequent at approximately 7400 years cal BP and not in the early Holocene, as found for the Campos Gerais and de São Francisco de Assis records. This likely is due to both the occupation by native Americans (Dillehay et al. 1992), who used fires to hunt (Leonel 2000), and seasonality in climate, which could have led to flammable biomass accumulation. The clear increase in fire frequency over different time frames suggests that humans came to occupy the plateau region later and that frequent fires during the Holocene were anthropogenic, facilitated by grasses. The presence of fast-growing grasses likely led to large amounts of flammable biomass accumulation during their growing season (Pillar and Quadros 1997). High numbers of Poaceae and a decline in other grassland taxa suggest the fire frequency may have also led to changes in the floristic composition of grasslands (Bond and van Wilgen 1996).

Carbonized particles appeared less frequently in sediments from the Cambará do Sul core from 1100 years cal BP on. The grassland area near the peat bog got smaller due to the expansion of *Araucaria* Forest, and fires became rare during the late

Holocene. However, the high abundance of charcoal particles indicates that fires were still frequent in the region. Late Holocene fire frequency was also documented in other sedimentological deposits, where the current vegetation comprises forest-grassland mosaics (Behling 1997; Behling et al. 2005, 2007).

The Cambará do Sul records document not only the impact of human-induced fires but also an increase in Poaceae pollen grains around 170 years cal BP (1780 AD), followed by the rise in the number of Cyperaceae around 100 years cal BP (1850 AD). This indicates a post-Colombian disturbance in the *Araucaria* Forest, possibly caused by cattle entering the forest areas. In the first decade of the eighteenth century, cattle were introduced by the Jesuits in the plateau region (Porto 1954); the city of Cambará do Sul was founded in 1864 with its economy based on cattle ranching. When grazing freely in the grasslands, cattle find refuge in the forest. The first *Pinus* sp. pollen grain ever found in the region dated around 130 years cal BP or 1820 AD. The time frame coincides with the arrival of the first German settlers in lower part of the highlands of Rio Grande do Sul, who likely introduced the exotic species. A reduction of *Araucaria angustifolia* pollen was detected between 30 and 15 years cal BP (1920 to 1935 AD), marking the beginning of a vast selective deforestation in the region. A massive reduction in *Araucaria* pollen (going from 41% to 2% at 3.5 cm deep in the profile) began around 10 years cal BP (1940 AD), which was intensified during the last 60–70 years, but not in the area around the peat bog where the core was taken. Other tree species, especially *Mimosa scabrella*, a few Myrtaceae species, *Lamanonia speciosa,* and *Ilex* sp., became more frequent, forming a secondary vegetation due to cattle entering the forest and the *Araucaria* logging. Tree ferns, *Dicksonia sellowiana*, were also removed from the *Araucaria* Forest during the past 60–70 years for commercial reasons, as their trunks were used to make pots for orchids and other ornamental plants.

We can conclude that the charcoal particle increase during the Holocene indicates anthropogenic fires, at first caused by native Americans and later by European settlers. Furthermore, cross-analyses of charcoal particles and pollen taxa at Morro Santana close to Porto Alegre (Behling et al. 2007) suggest that burning occurred in grassland areas and was not post-deforestation or for agriculture-related fires. Our studies also indicate an overall forest encroachment trend at Morro Santana, starting around 620 to 540 years cal BP (1330 to 1410 AD), with rapid changes, and transition periods around 380 to 300 years cal BP (1570 to 1650 AD) and between 60 and 20 years cal BP (1890 to 1930 AD). It is hard to tell apart anthropogenic and climate-driven changes once forest expansion was favored by climate but also affected by shifts in the disturbance regimes in the area. At first, these disturbances may have been caused by the native American population movement after the arrival of the Portuguese settlers and the cattle introduction in the seventeenth century. The impact of the Guarani populations is still unclear but likely small, given that they used forested areas, not grasslands, for agriculture. On the other hand, extensive cattle ranching, which directly impacts the vegetation through biomass removal and trampling, was the main activity of the European settlers. This type of land use controls forest encroachment by preventing certain forest saplings from resprouting (Pillar and Quadros 1997). The lack of palynological and charcoal evidence for the time of the first settlers, around 1740 AD, indicates they likely had little impact on vegetation dynamics and fire frequency. Feral cattle probably impacted vegetation much earlier, being the main driver of the pollinic transition period that ended at 300 years cal BP (1650 AD).

The sample extracted from Morro Santana delivers information on vegetation, climate, fire dynamics, and human activity during the past 1230 years cal BP (Behling et al. 2007). The development of a shallow bog and the sedimentological accumulation is related to changes in humidity, similar to what has been documented for the plateau region during the same time frame. Palynological data confirm the existence of grasslands in the region since the early Holocene, suggesting that the current small grassland areas surrounded by forests can be considered natural and not a by-product of deforestation and cattle introduction. During the late Holocene, forests successfully expanded under more humid climate conditions in the last 580 years cal BP.

4.7 Conservation of the South Brazilian Grasslands and Implications from Paleoecological Studies

Paleoecological and paleoenvironmental data about vegetation dynamics, fire, human impact, and land use in the southern Brazilian Plateau region provide crucial information for grasslands conservation and management. Several palynological records show that the highly diverse grassland areas are natural, i.e., remnants of an extensive area from the glacial period and the early and mid-Holocene, not from past forested areas. With that in mind, we suggest that grasslands should be protected and not submitted to afforestation, as is happening now, where large areas are planted with *Pinus, Eucalyptus,* and *Acacia*.

Palynological data show that grasslands were drastically reduced by the *Araucaria* Forest expansion, especially during the past 1100 years, over climate shifting to more humid conditions. The natural *Araucaria* Forest expansion, which is usually not possible due to human interference, would currently reduce the grassland areas. Several studies show that by excluding grazing and fire, the *Araucaria* Forest tends to expand over grasslands (Oliveira and Pillar 2004; Duarte et al. 2006).

Data on charcoal particles indicate that natural fires caused by lightning were rare in the southern Brazilian grasslands. Fire frequency probably started to increase due to the arrival of the first native Americans in the late Pleistocene, or after 7400 years cal BP, as observed in the Cambará do Sul region. Management and conservation plans must consider that manmade fire had an important role during the Holocene and certainly led to floristic changes. Some of the current plant communities could have adapted to fire (Overbeck et al. 2005). Besides, increased charcoal particles coincided with decreased plant diversity in the Campos (Behling and Pillar 2007). To what extent those two facts are related is yet to be determined; at any rate, climate change and the extinction of large grazing mammals are key aspects affecting biodiversity. Pollen data show that the late expansion of the

Araucaria Forest was possible despite the high fire frequency, but that then fire became almost absent from areas surrounding the study site in Cambará do Sul because of forest expansion. However, data from other regions where forest--grassland mosaics still exist point to the frequent fires.

The consequences of suppressing fire and grazing in conservation areas with forest-grassland mosaics in the southern Brazilian Plateau should be carefully pondered. Studies show that human disturbances have historically inhibited forest expansion; in their absence, grasslands will rapidly shrink until they finally disappear. From our point of view, grasslands deserve to be conserved, not driven to extinction solely because they do not correspond to the current climate and need human intervention to thrive. Furthermore, fire and grazing suppression produces a massive accumulation of flammable biomass, severely increasing the risk of catastrophic and unmanageable fires that can have unpredictable consequences on biodiversity (see also Pivello et al. 2021). Cattle ranching is another option for grassland management (Baggio et al. 2021), which could be a better and safer alternative to fires in managing grassland areas, avoiding negative outcomes such as soil degradation, air pollution, and the risk of uncontrollable fires. The large grazers that inhabited the southern Brazilian grassland until the early Holocene may have had an important role in maintaining their high plant diversity, similar to modern-day cattle. At any rate, the analyses of the role of fire and grazing in the past gives important indications of key drivers of grassland composition and dynamics. We know that climate change will increase, and certainly will have effects on forest-grassland dynamics – at least where natural vegetation is still present. This makes knowledge on the relation between climate and vegetation in the past very valuable.

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Chapter 5
A Historical Perspective on the Biogeography of the Pampa Region: Imprints of Time and Origins of Its Flora

Mabel R. Baez-Lizarazo, Matias Köhler, and Marcelo Reginato

5.1 Introduction

Open ecosystems such as grasslands, savannas, and shrublands cover up to 40% of the Earth's land surface (Gibson 2009), and are extremely relevant both to food production as to provisioning of ecosystem services, including net primary production, regulation of carbon, and water cycling (Vitousek 2015). These ecosystems are frequently thought of as representing ancient habitats, even before angiosperms dominate terrestrial ecosystems (Coet et al. 1987; Bredenkamp et al. 2002). However, extant grasslands are floristically dominated by species of grasses (Poaceae), as well as other diverse angiosperms families such as the daisies (Asteraceae), legumes (Fabaceae), sedges (Cyperaceae), and many others with minor contributions in species number (Bond 2019).

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In light of diverse types of data, including fossils and modern phylogenetic comparative methods, much has been proposed about the origins and evolution of grassland ecosystems. Current knowledge has pointed out that the rise of grasslands is linked to atmospheric CO_2 decline in the late Paleogene, ca. 34 Ma ago (Palazzesi et al. 2022). However, a multistage process involving continent-specific patterns must be taken into account (Strömberg 2011). According to this, after the Paleogene appearance of C_3 open-habitat grasses, a more recent expansion of C_4 grass lineages during the late Miocene (~10 Ma) has much impacted and shaped the grass-dominated habitats at tropical-subtropical latitudes (Jacobs et al. 1999; Bredenkamp et al. 2002; Spriggs et al. 2014). Specifically in South America, few studies have been carried out regarding the age, diversification, and the role of biotic interchange in open ecosystems. For the high-elevation grasslands in the northern Andes (Páramos) and the *campo rupestre* in central and eastern Brazil, a relatively recent diversification of the endemic component was detected (Torres et al. 2013; Madriñán et al. 2013; Vasconcelos et al. 2020), while multiple dispersals from other regions have been estimated for the Cerrado in Central Brazil (Simon et al. 2009; Antonelli et al. 2018; Azevedo et al. 2020).

The region that surrounds the *Río de la Plata* estuary in southern South America – the *Río de la Plata* grassland region sensu Soriano et al. (1991; hereafter, we use the term Pampa) – covers the vast plains of central-eastern Argentina (*Pampas* subregion), Uruguay, and southern Brazil (the latter two forming the *Campos* subregion). The area is characterized by spatially heterogeneous subtropical and temperate grassland and shrubland, with primary vegetation corresponding to mesophytic grasslands with a mix of C_3 and C_4 perennial grasses (Burkart 1975; Soriano 1991; Andrade et al. 2019), representing one of the most diverse, largest, and neglected open ecosystem in the world (Soriano et al. 1991; Overbeck et al. 2007; Boldrini 2009; Andrade et al. 2018). The Pampa has a high diversity of vascular plant species (4368 native species), with about 8% of the species endemic (403 spp.) (Andrade et al. 2018). However, the origin of the Pampa flora, their biotic interchange, dispersal timing, and local radiations remains poorly known. In particular, we lack an understanding of which regions served as primary sources of the vascular plants to the Pampa and which regions received lineages from this region. Previous phytogeographic studies suggest that the Pampa flora has links to other open formations of South America, such as Cerrado, Andes, and Chaco (Cabrera 1951, 1976; Rambo 1954; Waechter 2002; Fiaschi and Pirani 2009). Nonetheless, current evidence from biogeographic analyses of Neotropical biotas has shown that about 50% of dispersal events involved transitions heading from forested to open biomes (Antonelli et al. 2018).

How the set of species of an area was configured and what their biotic connections were are recurrent questions in historical biogeography and evolutionary biology (Pennington et al. 2004). Each biogeographical region (or bioregion) constitutes a species pool influenced by differences in speciation and extinction rates, and immigration from other regions over time (Pennington and Dick 2004). However, explaining the dynamics of the biotic interchange of the Pampa and other regions is challenging. Here, we attempt to first address this question by integrating a comprehensive dated phylogeny of angiosperms, species occurrence datasets, and models of geographical range evolution, to understand the evolution and connectivity of the angiosperm flora of the Pampa through time. We gathered data from the literature and public repositories regarding their occurrence in the Pampa region, and phylogenetic information when available. Hereby, we assess major patterns of distribution and richness in the Pampa, and historical connections between the Pampa and other surrounding Neotropical domains, by comparing sampled lineages regarding their origin, dispersal routes, and sympatric events related to the Pampa.

5.2 Material and Methods

5.2.1 Species Sampling and Distribution

In order to infer dispersal events and geographical range evolution in the Pampa and neighboring areas, species sampling was based on the taxa included in a comprehensive dated phylogeny of seed plants (Smith and Brown 2018). The only modifications to the original tree included removing all gymnosperms, as well as duplicated terminals of the same species, terminals identified as "cf." or "aff.", and terminals identified at the generic level. Our filtered working phylogeny included a total of 70,040 terminals/species out of the 79,881 terminals included in the original phylogeny.

All species in the chronogram were scored as present or absent in the Pampa and neighboring regions of interest: Andes, Cerrado, Chaco (including the Espinal and the Monte), and Atlantic Forest. Species not found in those neighboring areas were coded as "Others". Biogeographical area boundaries were retrieved by merging a more general classification of ecoregions from the WWF ecoregions shapefile (Olson et al. 2001), with a more specific and widely used classification for the focal area, the Pampa (Soriano et al. 1991, as *Río de la Plata* Grassland). Since Olson et al. (2001) consider the Pampa (sensu Soriano et al. 1991) as two distinct ecoregions within distinct biomes (i.e., Tropical and Subtropical Grasslands, Savannas, and Shrublands; and Temperate Grasslands, Savannas, and Shrublands), we unified these regions following the boundaries proposed by Soriano et al. (1991), but kept the others adjacent ecoregions from Olson et al. (2001). However, we did not score the classifications within the Pampa as '*Campos´* or *´Pampas*', as proposed by Burkart (1975) and followed by Soriano et al. (1991), in our matrix for analyses but used those definitions for the description and discussion of our results. Therefore, our distribution matrix included 70,040 species coded in six areas: Pampa, Andes, Cerrado, Chaco, Atlantic Forest, and Others (Supplementary File S5.1). Presence was coded as follows for each area: Andes (4984 spp.), Cerrado (2969 spp.), Chaco (1012 spp.), Pampa (1539 spp.), Atlantic Forest (4388 spp.), and Others (66328 spp.).

Geographical coding was based on several datasets, including distribution records and floras or checklists of the areas of interest. First, the geographical distribution of all terminals was gathered from POWO (2022), and species present in Pampa, Andes, Cerrado, Chaco, and Atlantic Forest regions (core areas) were flagged, while the species not present in those areas were classified as endemic to the “Others” area. Presence or absence in the core areas was then coded based on the species distribution points from GBIF.org (2021). Points were retrieved using the R package rgbif v.3.6.0 (Chamberlain et al. 2021), and extensively filtered as described in Reginato et al. (2020). Coding refinements for species in each area or coding for species with no points available was then performed with information of local floras or checklists (Andrade et al. 2018; Bonifacino et al. 2020; Flora do Brasil 2020; Catálogo de las Plantas Vasculares del Conosur 2021; Deble 2021; Grattarola et al. 2020; González et al. 2018; Gonzatti et al. 2021; Guerrero et al. 2018; Keller et al. 2021; Külkamp et al. 2018; Mendoza-Díaz et al. 2020; Pasini and Miotto 2020; Plá et al. 2020; Valtierra et al. 2021). All taxonomic names in the phylogeny, distribution points, and checklists were homogenized according to accepted taxa in GBIF.org (2021).

Richness distribution maps of sampled species at 0.5 degrees of spatial resolution (all species present in the Pampa and endemics to the Pampa) were generated with the filtered points using the R package monographaR v.1.2.1 (Reginato 2016). Not all species included in the analyses had geographical points, thus the richness map included 99% of the species coded as present in the Pampa (1527 out of 1539), and 69% of the species coded as endemic to the Pampa (24 out of 35). Venn diagrams of the number of sampled species shared between Pampa and the other areas based on the presence/absence matrix were generated using the R package ggvenn v. 0.1.9 (Yan 2021).

5.2.2 Ancestral Range Distribution

Ancestral range distribution was estimated with maximum likelihood as implemented in the R package BioGeoBEARS v.1.1 (Matzke 2013). The filtered chronogram and the presence/absence matrix were used in these analyses. The maximum range size parameter was set to the total number of areas in the matrix (=6). The best-fit range evolution model was estimated through Akaike’s information criterion (AIC) comparison in BioGeoBEARS. Two models of range evolution were compared: DEC (AIC = 133533.6) and DEC + J (AIC = 133303.1). The best-fit model (DEC + J) was used for the ancestral range estimation. Results were summarized, including information on the number of events, age of dispersals, and other descriptive results, with BioGeoBEARS and ape v.5.4 (Paradis and Schliep 2019).

5.3 Results

Of the 4175 native flowering plant species currently reported for the Pampa, we gathered phylogenetic and geographical distribution data of 1539 (36%). This sampling revealed an uneven distribution of plant richness across the Pampa region

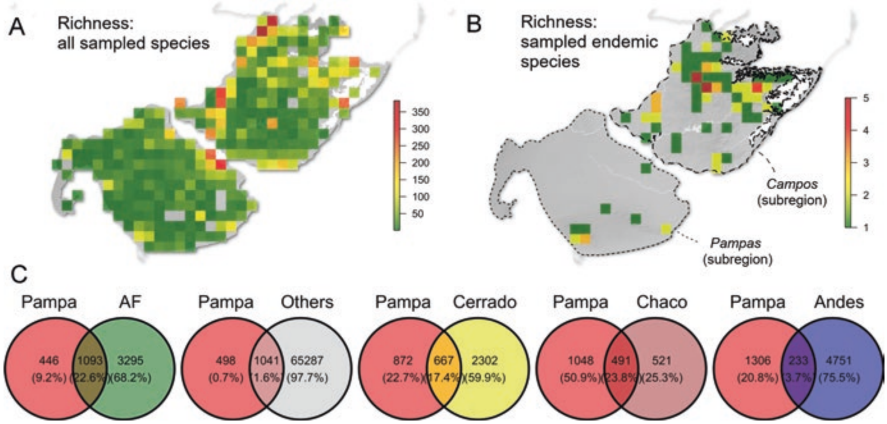

Fig. 5.1 Overview of the geographical distribution of the species sampled in this study. (**a**) Richness distribution of all sampled species with occurrence in the Pampa. (**b**) Richness distribution of sampled species endemic to the Pampa. Both richness maps at 0.5 degrees of spatial resolution. (**c**) Venn diagrams showing the number of shared species between the Pampa and the other analyzed areas (numbers refers only to sampled species). *AF* Atlantic Forest

(Fig. 5.1a). Most of the richness is concentrated in the northern and northwestern of the *Campos* subregion in the south of Brazil (Rio Grande do Sul state), Uruguay, and Argentina (part of the Corrientes province). On the other hand, the *Pampas* subregion in Argentina showed in general lower species richness, with a notable exception in part of the Rolling Pampa near the Rio de La Plata estuary. Overall, the distribution of endemism richness also followed an uneven pattern (Fig. 5.1b), and the majority of the plant endemism richness revealed is in the *Campos* subregion, especially in the transition region of Brazil and Uruguay.

The bulk of the Pampa angiosperm flora sampled here is shared with the Atlantic Forest (1093 species, 71% of the species sampled in the Pampa; Fig. 5.1c), and also with other biogeographic regions not scored in our study ('Others', 1041 spp., 67%). Almost half of the Pampean flora here sampled is also shared with the Cerrado (667 spp., 43%), followed by minor parts with the Chaco (491 spp., 31%) and the Andes (233 spp., 15%).

Our biogeographic analyses estimated 2146 events involving the Pampa as an ancestral area across the phylogeny – either as a single area or within a wide ancestral range (including other biogeographic regions). This information is summarized in Fig. 5.2, with the nodes involving the Pampa as an ancestral area highlighted, while all the ancestral estimates are provided in Supplementary File S5.2. Most of the estimated events were dispersals (1515 events, 70.6% of all events), while vicariance or subsets amount to ca. 6% (134 events), and sympatric events to ca. 23% (497). Among the latter, a total of 30 sympatric events are estimated to be within the Pampa only (i.e., excluding events with widespread ranges). A list of those events, including age and taxa involved, is available in Supplementary File S5.3, while a histogram of their ages is presented in Fig. 5.3e. Although a few sympatric events

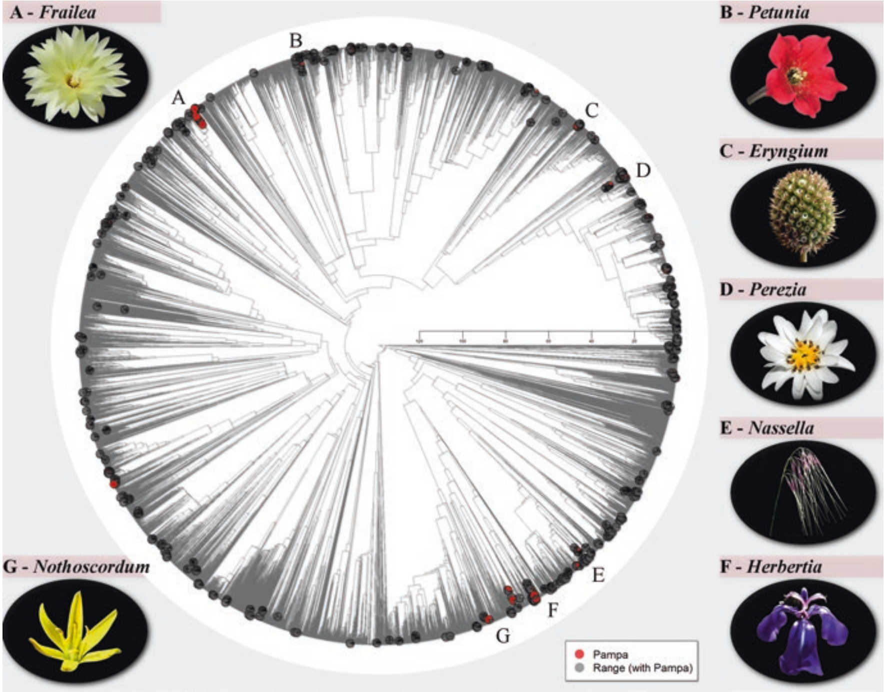

Fig. 5.2 Maximum likelihood estimate of the historical biogeography of angiosperms under the DEC + J model. Pie charts at the nodes represent the probability of ancestral range estimates; only pie charts of nodes with estimates in the Pampa or a range including the Pampa are shown; colors following the legend. Selected lineages with ancestral estimates in the Pampa (in situ diversification) are depicted in (**a**–**g**). (**a**) *Frailea* (Cactaceae). (**b**) *Petunia* (Solanaceae). (**c**) *Eryngium* (Apiaceae). (**d**) *Perezia* (Asteraceae). (**e**) *Nassella* (Poaceae) (**f**) *Herbertia* (Iridaceae). (**g**) *Nothoscordum* (Amaryllidaceae). Photo credits: all from MRBL, except *Nassella* (MK) and *Perezia* (Sérgio Bordignon)

were recovered from the Pliocene (~5–2 Ma), most of the sympatric events within the Pampa are very recent, dating from the Pleistocene (2 Ma onward, Fig. 5.3e). Some remarkable sympatric events within the Pampa recovered here include clades from Asteraceae (*Microgyne*, *Perezia*, *Sommerfeltia*, and *Stenachaenium*), Apiaceae (*Eryngium*), Cactaceae (*Frailea*, *Gymnocalicium,* and *Parodia*), Amaryllidaceae (*Nothoscordum*), Solanaceae (*Calibrachoa* and *Petunia*), and Iridaceae (*Calydorea*, *Cypella*, and *Herbertia*).

A high asymmetry is observed between dispersals from the Pampa to the remaining areas (94 dispersals), and from other areas to the Pampa (1619 dispersals). A summary of the estimated direction of the dispersal events and their associated ages are depicted in Fig 5.3a, c, d, f). Most of the dispersals toward the Pampa region were estimated to be from the 'Others' area (i.e., outside the core analyzed areas; with 1083 dispersals). Among the core areas, source areas to the Pampa flora were recovered in decreasing order as from the Atlantic Forest (252 dispersals), Andes

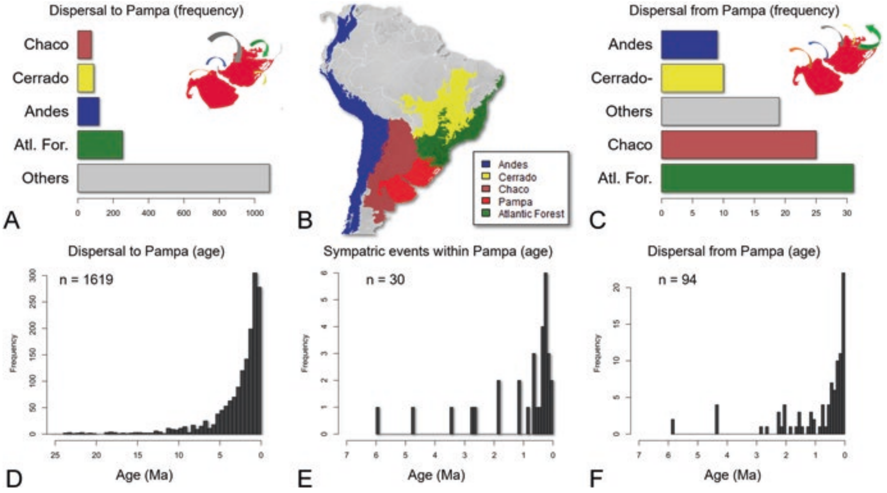

Fig. 5.3 Summary of the estimated events (dispersals and sympatry) involving the Pampa. (**a**) Barplot showing the frequency of dispersals to Pampa. (**b**) Biogeographical scheme analyzed in this study. (**c**) Barplot showing the frequency of dispersals from Pampa. (**d**) Histogram showing the age (x-axis) of dispersal events to Pampa. (**e**) Histogram showing the age (x-axis) of sympatric events within Pampa. (**f**) Histogram showing the age (x-axis) of dispersal events from Pampa. Colors in (**a**) and (**c**) follow the map and the legend (**b**)

(119), Cerrado (89), and Chaco (76). The areas that received lineages from the Pampa region were revealed as the Atlantic Forest (31 dispersals), Chaco (25), Others (19), Cerrado (10), and the Andes (9). Regarding the age of the dispersal events toward the Pampa (Fig. 5.3d), there is an increase of events at the end of the Miocene, from the Pliocene onward (ca. 5 Ma). On the other hand, dispersals from the Pampa (Fig. 5.3f) are more scattered and concentrated from the last 2 Ma toward the present (Pleistocene onward).

5.4 Discussion

5.4.1 Patterns of Richness and Distribution of the Pampean Flora

The Pampa region is under a continuous, rapid, and profound land cover change pressure, whereas in the past 20 years at least 8% of its natural grassland areas were lost due to farming and forest plantation expansion (Baeza et al. 2022). Nonetheless, it still represents one of the largest, most diverse, and historically less transformed grassland areas in the world, harboring more species per unit area than the Southern Cone of South America (Argentina, Chile, Paraguay, southern Brazil, and Uruguay), and nearly equal to the Cerrado, the largest continuous tropical grassland and savanna region in the Americas (Andrade et al. 2018; Oyarzabal et al. 2019). It has been suggested that such high species richness is probably due to its location in a transition zone between other major Neotropical areas (Burke et al. 1998), but local climatic conditions, soil types, and grazing intensity may have also been influencing plant diversity (Paruelo et al. 1995; Berretta et al. 2000). Overall, such features confer highly heterogeneous habitats, both physiognomically and floristically. Our analyses revealed higher species richness and endemism in the *Campos* subregion, with decreasing numbers toward the Argentinean *Pampas* subregion. This is congruent with previous reports and has been explained by a latitudinal and environmental gradient, with a reduction in soil water and lower environmental heterogeneity in terms of geology and topography toward the south (Soriano et al. 1991; Paruelo et al. 2007; Andrade et al. 2018; Oyarzabal et al. 2019). These characteristics are also highlighted in the regions with high endemism levels, which were featured especially in heterogeneous environments such as the Serra do Sudeste and other shallow soils habitats in Rio Grande do Sul, and the Sierra Tandilia and Sierra de la Ventana in Argentina. Furthermore, the Northern *Campos* makes contact with more diverse bioregions that may influence its species pool – such as the Atlantic Forest, Seasonally dry Tropical Forests (SDTF), and Chaco (including the Espinal), while the boundaries of the southern Pampa include mostly the Chaco (the Espinal and the Monte).

The bulk of the angiosperm species of Pampa is shared with the Atlantic Forest and with our group of 'Others'. This suggests that an important proportion of the species might be shared with areas further distant or areas that have not been stressed in the literature as with important connections with the Pampa. Although the Pampa is overall dominated by grasses and other herbaceous taxa, the presence of trees and woody plants is noteworthy. These species are especially found in certain topographic conditions that provide relatively high water availability or protection from disturbances, such as corridors along the stream and rivers basins (riparian forests) and rocky slopes (Mourelle et al. 2017). Such features might explain the high number of species shared with the Atlantic Forest domain (Oliveira-Filho et al. 2015; Rezende et al. 2016). Additionally, the Atlantic Forest also exhibits notable areas of open ecosystems, such as the highland grasslands (*South Brazilian highland grasslands* and *Campos de Altitude*; Vasconcelos 2011; Overbeck et al. 2022), that, despite their unique floristic composition and environmental features, share many species with the Pampa grasslands (Andrade et al. 2018).

Confirming previous phytogeographic studies and hypotheses (Cabrera 1951, 1976; Cabrera and Willink 1980; Rambo 1954; Burkart 1975; Waechter 2002; Fiaschi and Pirani 2009), a notable part of the Pampean flora is shared with the Cerrado, the Chaco, and the Andes. Members of several families (such as Poaceae, Myrtaceae, Apocynaceae, Solanaceae, Ericaceae, Apiaceae, Orchidaceae, Asteraceae, and Fabaceae) that are typical in the central savanna of Brazil (Cerrado), but have their southern distribution limit in the Pampa region (Rambo 1954; Boechat and Longhi-Wagner 2000). The links between the Pampa and the Chaco flora are also remarkable, where a sequence of species impoverishment from the Chaco toward the Pampa has been proposed by Cabrera (1976) and Cabrera and Willink

(1980). With minor expressions but still notable, part of the Pampa flora is also found in the Andes. The floristic element of the Andes in the Pampa, which actually extends further to the *South Brazilian highland grasslands*, are well documented for several species of Asteraceae, Calyceraceae, Gunneraceae, Campanulaceae, Ericaceae, Fabaceae, Onagraceae, Rosaceae, and Poaceae (Arroyo et al. 1996; Armesto et al. 1995; Waechter 2002; Iganci et al. 2011).

5.4.2 Biotic Exchange Between Pampa and Neighboring Areas

Exchange of lineages between the Pampa and the analyzed areas involved a great direction asymmetry, with the greater of the events being toward the Pampa, while dispersals from the Pampa to other areas were less frequent. This result suggests that the Pampa may represent a macroevolutionary sink (Goldberg et al. 2005). A rampant number of dispersal events from areas that are not traditionally related with neither neighbors to Pampa ('Others') were recovered in our analyses. Despite putative issues with sampling (see next section), this result might reinforce the role of long-distance dispersals in the assembly of the Pampa flora, which, although intriguing, is increasingly reported as shaping many patterns of plant distribution across the Neotropics and beyond (Pennington et al. 2004; Clayton et al. 2009; Hughes et al. 2013; Christenhusz and Chase 2013; Harris et al. 2018; Frankiewicz et al. 2022).

In concordance with the patterns of species distribution shared with other major neighboring regions, the Pampa had a remarkable biotic exchange with the Atlantic Forest, Chaco, Cerrado, and the Andes. Following the imperative numbers of dispersal from the 'Others' area to the Pampa, the Atlantic Forest has a noticeable role in the events shaping the Pampa flora. Similar results have been reported in other Neotropical open ecosystems (Simon et al. 2009; Azevedo et al. 2020), reinforcing that dispersal events involving transitions heading from forested to open biomes are important in shaping Neotropical assemblages (Antonelli et al. 2018). Nonetheless, given the heterogeneous nature of the Pampa region, further studies should track this influence on the woody vs. herbaceous component. We also recovered notable dispersal events from the Pampa to the Atlantic Forest. Most of these events may be related to the colonization of the highland grasslands (*South Brazilian highland grasslands* and/or *Campos de Altitude*), where known cases have already been reported (Reck-Kortmann et al. 2014, 2015; Mäder et al. 2013; Mäder and Freitas 2019). These results reinforce the narrow relationship between the Pampa and highland grasslands of southern Brazil, which together – and also in this book – often are considered as the South Brazilian grasslands (Andrade et al. 2019).

While biotic connections between the Pampa and the Cerrado are still poorly known (Werneck et al. 2012; Azevedo et al. 2020), connections with the Andes and the Chaco have been studied. The Peripampasic Orogenic Arc (Frenguelli 1950) – formed by a mountains chain from the Cordillera Oriental, the Sierras Subandinas, and the Sierras Pampeanas, Sierra of Buenos Aires, linking Argentina, Uruguay, and Brazil – is thought as an important connection proposed to explain the presence of

Andean and Chaquean species in the Pampa (Kurtz 1904; Frengüelli 1950; Morello 1958; de la Sota 1967; Crisci et al. 2001; Morrone 2001; de la Sota et al. 2004; Ferretti et al. 2012; Moreno et al. 2018; Köhler et al. 2020). Species of Andean origin, which dispersed through Argentina and Uruguay, have their northernmost limit in the southeastern Rio Grande do Sul (Brazil), such as species of the genera *Melica* and *Stipa* (Boldrini 2009*),* as well as species of lichens (Garcia and Palacio 2021), pteridophytes (de la Sota et al. 2004), spiders (Ferretti et al. 2012), and gastropods (Dos Santos et al. 2021).

5.4.3 In Situ *Diversification and the Timing of Pampa Flora Assemblage*

Our analyses identified 30 lineages that likely diversified within the Pampa, i.e. the Pampa is the putative ancestral area of cladogenetic events. Most of these lineages have remarkable species richness in the Pampa grasslands, some including endemic species, such as members of Amaryllidaceae (*Nothoscordum*), Apiaceae (*Eryngium*), Apocynaceae (*Oxypetalum*), Asteraceae (*Perezia*, *Stenachaenium*, *Hypochaeris*, *Sommerfeltia*, *Microgyne*), Cactaceae (*Frailea*, *Parodia*, *Gymnocalycium*), Euphorbiaceae (*Croton*, *Tragia*), Iridaceae (*Herbertia*, *Cypella*, *Sisyrinchium*), Solanaceae (*Calibrachoa*, *Petunia*), Orchidaceae (*Bipinnula*), and Poaceae (*Distichlis*, *Hordeum*, *Nassella*). The majority of these cladogenetic events were recovered in the past 5 Ma, with a greater concentration of events in the Pleistocene (the last 2.6 Ma). Regardless of debates if speciation can occur in this relatively short geological time, there is now overwhelming evidence that Quaternary plant speciation occurred frequently (Kadereit and Abbott 2022). This period is known by climatic oscillations, which resulted in glacial and interglacial periods, affecting sea-level oscillations (e.g., marine regression), selective pressure of pollinators, and the expansion of ancestral areas with subsequent fragmentation and isolation of populations. Most of the studies involving species that occur in the Pampa have congruent results regarding the age of events and related phenomena that may have influenced their distribution or genetic structures. Examples include *Eugenia uniflora* (two clades that diverged c. 4.9 Ma; Turchetto-Zolet et al. 2016); the most recent common ancestor of *Petunia* and *Calibrachoa* (5 Ma; Mäder et al. 2013; Mäder and Freitas 2019), with divergence processes intensifying between 2.8 and 0.4 Ma in *Petunia* (2.8–1.1 Ma; Särkinen et al. 2013, Lorenz-Lemke et al. 2010); *Turnera sidoides* (2 Ma; Moreno et al. 2018); *Cereus hildmannianus* (1.45–0.19 Ma; Silva et al. 2018); and *Calibrachoa heterophylla* (0.4 Ma in Mäder et al. 2013).

The ages shaping the bulk of events (dispersals and in situ diversifications) in our analyses are notably during the last 5 Ma. Macrofossil and palynological evidence from the region indicate that herbaceous vegetation in the Pampa was present since the Middle Miocene, and dominant until after 7 Ma (Jacobs et al. 1999; Ortiz-Jaureguizar and Cladera 2006; Strömberg 2011). During the Pliocene through the Pleistocene (5.32–2.58 Ma), grasslands, steppes, and shrublands dominated the region associated with a rich fauna of megaherbivores accompanied by drier and cooler conditions (Burkart 1975; Ortiz-Jaureguizar and Cladera 2006; Barnosky and Lindsey 2010). In more recent times, especially from the Pleistocene onward, the fossil record indicates a drastic modification in the taxonomic and ecological composition of the Pampa flora, from the onset of more humid and stable climatic conditions, and the expansion of non-grasses pollens (Prieto 1996; Iriondo 1999; Prieto 2000; Iriarte 2006; Ortiz-Jaureguizar and Cladera 2006; Behling et al. 2005, 2007, 2009; Chaneton et al. 2012). Altogether, these observations are consistent with our findings, which recovered a small number of old in situ speciation events in the Pampa and a greater lineage turnover from the Pliocene onward.

Evidence suggests that today's Pampa is a relict of drier past climates in the region, which has allowed the current dominance of grasses. However, the current climate is suitable for forests to grow, and there is evidence of tree encroachment across different Pampean regions (Chaneton et al. 2012 and reference therein). The lack of dominant arboreal vegetation is mainly explained by abiotic stress on the tree growth potential and biomass consumption by fire and herbivores (Bredenkamp et al. 2002; Bond 2008; Bond et al. 2005). Despite the remarkable feature of the Pampa region, land-use changes (e.g., conversion and intensive use for crop production, afforestation, and grazing) have been causing widespread loss and fragmentation of large areas of grasslands (Sala 2001; Gibson 2009; Overbeck et al. 2022), leading to biodiversity losses of local diversity and invasion of non-native species (Pillar et al. 2009; Staude et al. 2018; Andrade et al. 2018), and consequently hindering our understanding of the origin and evolution of the Pampa flora.

5.5 Caveats and Future Directions

Here, we provide a first comprehensive overview of the angiosperm historical biogeography in the Pampa and neighboring regions in South America. This initial attempt corroborates some long-standing views from phytogeography, such as a great number of lineages shared among those areas, as well as a great exchange of lineages among them. Our results are also in agreement with evidence from the fossil record, placing both lineage exchange (dispersals) and sympatric events (diversification) very recently in geological time (mainly concentrated in the Pliocene onward, with a great increase during the Pleistocene).

Nonetheless, we stress that several biases can affect this kind of study. Major issues include geographical area delimitation, phylogenetic estimation error, geographical distribution miscoding, and sampling problems. The latter, both in phylogenies and geographical distributional data, likely result in a putative underestimation of in situ diversifications in the Pampa, as well as of dispersals from this area to other regions. Although we used one of the most broadly inclusive seed plant phylogenies, several well-known typical Pampean groups are poorly represented in it. Examples of these include some genera with a high number of endemics in the Pampa (e.g., *Mimosa, Croton, Dyckia, Baccharis, Butia, Grindelia,* *Senecio, Euphorbia, Aristida,* and *Tillandsia*). Precisely, the current sampling analyzed here represented 37% (1539 spp. of 4175) of the native angiosperms species currently reported to the Pampa, including 9% of the known endemic species (Andrade et al. 2018). On the one hand, this suggests that further sampling is desired to improve the discussion of the Pampa floristic assembly, particularly to pinpoint whether the missing endemic species radiated in the Pampa or are scattered across their clades. On the other hand, this highlights that the Pampa is also a neglected region regarding phylogenetic sampling in comparison with other open areas (e.g., *campo rupestre*, Vasconcelos et al. 2020).

Although the availability of occurrence records has greatly increased in the past years (e.g., GBIF and SpeciesLink), as well as tools to deal with biases already known in these datasets (e.g., records of terrestrial species in the sea, records with coordinates assigned to the centroids of political entities or to institutions, or records of species in cultivation or captivity, Zizka et al. 2020), there is also the issue of geographical distribution miscoding. Improving automated geographical coding will depend on improving field collection, taxonomic work, and herbaria curation efforts. The availability of taxonomic work online has also greatly improved in the past years (e.g., Flora do Brasil and Species of Cono Sur). Thus, with new phylogenetic data, refined taxonomic and distribution data, the analyses presented here should be re-evaluated. Finally, a great portion of the events recovered in our analyses was related to the "Others" area. Thus, finer-scale analyses regarding area scheme delimitation might further uncover interesting patterns related to the origin of the Pampa flora.

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Chapter 6
Climate and Soil Conditions Across the South Brazilian Grasslands

Heinrich Hasenack, Gabriel Selbach Hofmann, Eliseu José Weber, and Eliana Casco Sarmento

6.1 Introduction

The South Brazilian grasslands extend over the three states of the southern region of Brazil, the states of Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS), a large and heterogeneous territory. They are under humid subtropical climate, Cfa and Cfb according to Köppen's classification (Alvares et al. 2013) (Fig. 6.1). This climatic condition is associated with the dynamics of atmospheric circulation usual in this subtropical region (24°S to 34°S) on the eastern coast of South America, which influences the availability of energy and water throughout the year.

The geological basement is the Mantiqueira Province, a region composed of crystalline rocks, which were submitted to faulting and folding because of the collision and separation of past continents during the Neoproterozoic Period of the Proterozoic Era and the Cambrian Period of the Paleozoic Era, between 950 and 540

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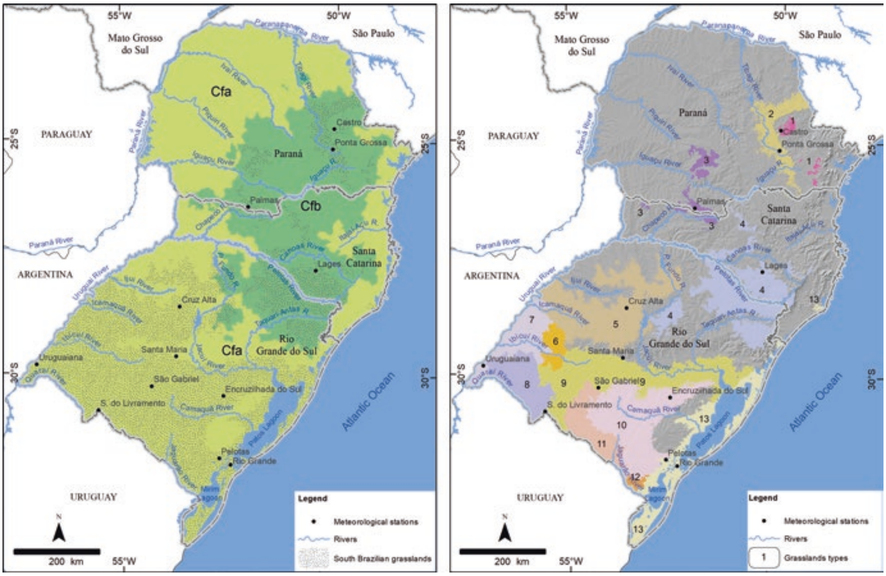

Fig. 6.1 Distribution of Köppen's Cfa and Cfb climates in the Southern Region of Brazil (modified after Alvares, 2013) and weather stations whose data were used to characterize different grassland areas of the south Brazilian grasslands; on the right, regionalization of South Brazilian grasslands: 1 Curitiba-Castro Grassland, 2 Ponta Grossa-Tibagi Grassland, 2 Guarapuava-Palmas Grassland, 4 Lages-Vacaria Grassland, 5 Aristida Grassland, 6 Sandy Grassland, 7 Park Grassland, 8 Shallow Soil Grassland, 9 Inland Sub-montane Grassland, 10 Bush Grassland 11 Shortgrass Grassland, 12 Atlantic Sub-montane Grassland, 13 Coastal Grassland. Terminology follows Hasenack et al. (2023)

million years ago (Ma) (see also Menegat 2023, Chap. 2 in this volume). The weathering and the action of glacial, fluvial, and aeolian erosion from the Paleozoic Era until the Jurassic Period of the Mesozoic Era (540 Ma to 145 Ma) formed a large sedimentary basin named Paraná Province. In the Cretaceous Period of the Mesozoic Era (145 Ma to 66 Ma), successive fissure volcanic eruption events covered this sedimentary basin with a sequence of mafic and felsic lava flows. In the Quaternary Period of the Cenozoic Era (400 ka to the present) the South Brazilian Coastal Plain was formed as a result of successive marine transgression events that reworked colluvial and marine sediments as well as alluvial plains especially along the large inland rivers (Bizzi et al. 2003, see Menegat 2023, Chap. 2 in this volume).

The changing climatic conditions acting on these geological structures sculpted different landforms over time and provided for the formation of a variety of soil types associated not only with their latitudinal position, but also with their situation in terms of elevation and slope. The result is a variety of biophysical conditions whose characterization contributes to the understanding of the distribution pattern of different grassland typologies in the South Brazilian grasslands (Hasenack et al. 2023). In the following, we will give an overview of the principal climatic characteristics and main functional soil classes in the region, thus facilitating the understanding of patterns of natural landscapes and biodiversity, but also to understanding, and planning, of land use.

6.2 Climatic Characteristics

6.2.1 Atmospheric Dynamics

The subtropical latitudinal position near the eastern coast of the Atlantic Ocean is a key factor in understanding the prevailing weather and climate patterns in Brazil's southern region (Nimer 1979; Grimm 2009a; Aquino 2012). This location provides considerable seasonal variation in incident solar radiation, resulting in a pronounced thermal contrast between the summer and winter months. In addition, the southern region of Brazil lies in a transition zone between two rainfall regimes. The South Brazilian grasslands are affected by both tropical and polar air masses and, therefore, the annual variability of meteorological elements depends largely on the maintenance or alteration of normal atmospheric circulation patterns.

The occurrence of teleconnection events induces a temporal variability in the thermal and rainfall regime in the South Brazilian grasslands. These events are anomalies generated by climate forcers that cause an imbalance in the global climate system, affecting the upper atmospheric circulation, and triggering meteorological anomalies in regions far away from their center of origin (Aquino 2012). The two main modes of climate variability on the interannual scale that affect the southern region of Brazil are the El Niño Southern Oscillation (ENSO) and the Southern Hemisphere Annular Mode (SAM). ENSO has two distinct phases, the warm (El Niño) and cold (La Niña) phases, related, respectively, to the warming and cooling of the surface waters of the Pacific Ocean. The change in Pacific Ocean water temperature triggers a series of feedback effects between ocean and atmosphere, leading to changes in normal atmospheric pressure and circulation patterns, moisture fluxes into the interior of South America, and intensity of the subtropical jet stream (Grimm 2009b). In the southern portion of the South Brazilian grasslands, the interactions between all these different factors result in increased rainfall during El Niño years, and reduced rainfall in La Niña events (Fontana and Berlato 1997). SAM, on the other hand, is a mode of climate variability related to the accumulation of ice on the Antarctic Peninsula, whose variations cause changes in westerly winds between latitudes 30°S and 60°S, which in turn affect rainfall and air temperature in the southeastern region of South America (Reboita et al. 2009; Aquino 2012; Schossler et al. 2018).

6.2.2 Main Climatic Elements

Climate can be characterized by the analysis and interpretation of several climatic elements, but the most ecologically relevant are those that express the availability of energy and water, such as solar radiation, temperature, precipitation, and evaporation. Based on these elements, records from meteorological stations located in different sites in the South Brazilian grasslands were used to describe and interpret subregional climatic conditions.

6.2.2.1 Solar Radiation

The incident solar radiation presents a sinusoidal variation throughout the year, due to the variation in the angle of incidence and the duration of the photoperiod. The lowest solar irradiation values occur in June and the highest in December, the months of the winter and summer solstices for the southern hemisphere, respectively. The difference between these two periods increases with latitude, from about 40% in the north of PR, and reaching up to 60% in the south of RS (Fig. 6.2).

Furthermore, the interception of solar radiation by the surface is influenced by the relief, which affects the thickness of the atmospheric layer over each location as well as slope and aspect of the terrain. Thus, the local effect of topography introduces spatial and temporal heterogeneity in the incident solar radiation (Carlucci et al. 2015). South-facing slope areas in the southernmost regions of the South Brazilian grasslands receive less energy during the year, while flat areas at high elevations or on north-facing slopes receive more solar irradiation. Local differences caused by topographic variations tend to be reduced during the summer months, when the angle of incidence is closer to the zenith, and amplified during the winter when it is steeper (Weber 2011). Variations in solar irradiation on different slope faces represent an important ecological factor, influencing both the species composition and the structure of plant communities in the South Brazilian grasslands due to the effects on fire-vegetation feedbacks (Blanco et al. 2014; Carlucci et al. 2015).

Cloudiness, i.e., the extent to which the atmosphere is covered by clouds, also influences the spatial and temporal variability in solar irradiation. In southern Brazil, cloudiness is higher close to the highland scarps that face east along the Atlantic Ocean's coast. The prevailing easterly winds bring moisture from the ocean, and the presence of the escarpment forces the moist air upward, where condensation generates fog and cloudiness, a fact also observed in escarpments in the interior of the states of SC and PR. Atmospheric attenuation intensified by more frequent cloud cover tends to reduce incident solar radiation and sunshine in regions with more cloudiness. Thus, the high cloudiness associated with high precipitation may be the explanation for the low rates of solar radiation and sunshine recorded in Palmas (southern PR), despite the lower latitude compared to other locations in the South Brazilian grasslands (Fig. 6.2).

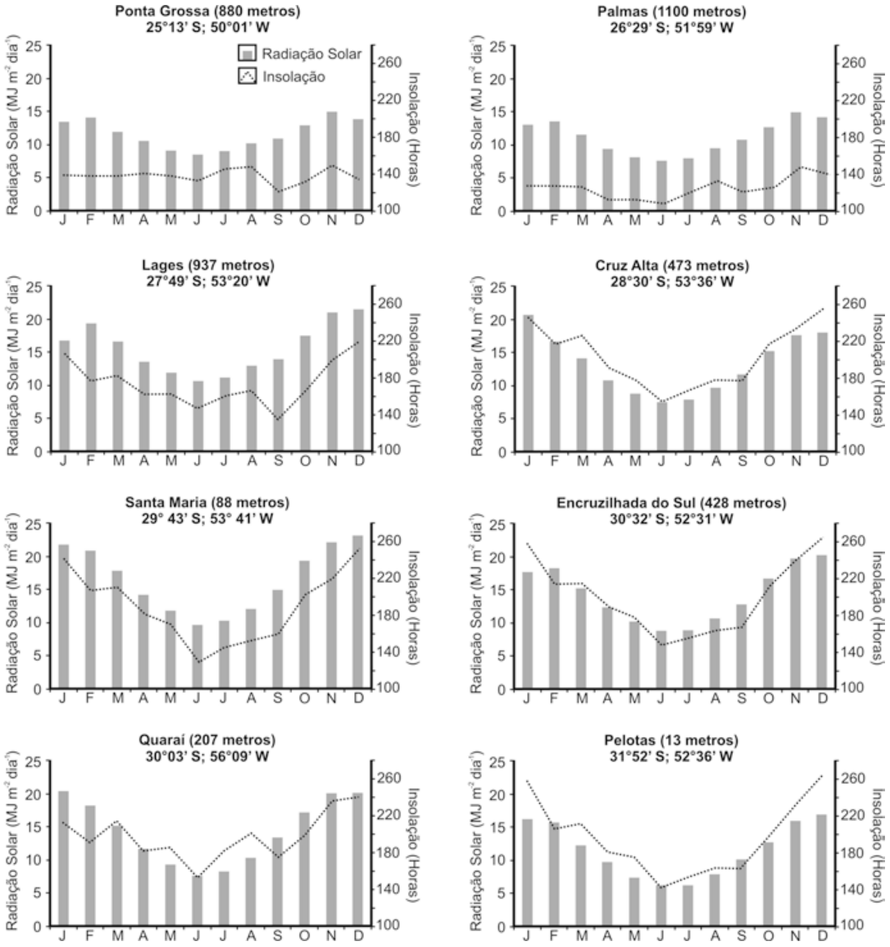

Fig. 6.2 Annual variation of global solar radiation and total sunshine at different locations in the South Brazilian grasslands. Gray bars represent monthly averages of global solar radiation (MJ.m^2.day^{-1}) and the dashed black line represents monthly averages of sunshine (hours). (Source of climatic data: Wrege et al. 2012)

The seasonal variation of cloudiness also causes important changes in the patterns of incident solar radiation. In RS, the period of greatest cloudiness occurs between June and September (de Custódio et al. 2009), a period when the diffuse fraction of solar radiation becomes predominant due to the decrease of the direct fraction by cloudiness (Weber 2011). This may be important for certain plant communities as the increase in diffuse fraction is normally associated with increased photosynthetic efficiency, with effects on biomass production (Sinclair et al. 1992).

6.2.2.2 Air Temperature

Although the southern region is the coldest in Brazil, the mean annual temperatures in the South Brazilian grassland region are higher when compared to those recorded in other grassland formations of the world, such as the steppes of eastern Europe or the prairies of North America. Nonetheless, between late autumn and early spring, frosts are frequent, especially in higher elevations (Wrege et al. 2012). Latitude and relief, and the synergy between them, as well as their interactions, are the main geographic determinants of temperature in southern Brazil and result in a pronounced thermal contrast between the plains and the higher areas (Nimer 1979). While latitude is associated with the distribution of energy, increasing altitude leads to a reduction in the heat retention capacity on the higher areas due to the lower thickness of the atmosphere.

The coldest areas of the South Brazilian grasslands are found on top of the South Brazilian Highland in Palmas (1100 m), and Castro (1000 m) in the state of PR, in Lages (937 m) in the state of SC, and in the northeastern part of RS (1100–1200 m). The highest peak of the region is the Morro da Igreja, in the municipality of Urubici, SC, with 1800 m. This colder portion is represented in Fig. 6.3 by the locality of Lages, whose monthly averages of absolute minimum temperature are below −5 °C during the winter quarter. Thus, the highest locations of the Southern Plateau are those that accumulate the greatest number of hours of cold and also record the greatest number of days with frost during the year, both in SC and in RS (Moreno 1961; Nimer 1979; Aguiar and Mendonça 2004).

The influence of the relief on the regional climate is also evidenced by the lower average temperatures in Palmas, located at an elevation of 1100 m, compared to those in higher latitude, but at lower elevation (Fig. 6.3). In contrast, the highest maximum temperatures occur in Quaraí, western Rio Grande do Sul, where the low elevation and higher continentality favor air warming (Nimer 1979; Firpo et al. 2012). In Fig. 6.3, this region is represented by Quaraí, although other nearby locations such as Uruguaiana and São Borja record even higher temperatures (Wrege et al. 2012). Finally, the Atlantic Ocean is also an important geographical factor, reducing the annual temperature range in coastal areas compared to locations of the same latitude farther west, on the border with Argentina (Moreno 1961; Nimer 1979). Coastal areas are also less susceptible to frost in winter (Aguiar and Mendonça 2004; Nimer 1979).

Atmospheric circulation likewise has great influence on the temperature patterns throughout the southern region of Brazil. During the fall and winter months, the region is frequently invaded by polar air masses coming from the Antarctic continent. The passage of these fronts is marked by prolonged rains covering a large extension, with the subsequent days characterized by high atmospheric pressure, clear skies, and low temperatures (Wrege et al. 2012). The lowest temperatures in the South Brazilian grasslands are usually recorded under these conditions, which can last for several consecutive days, thus characterizing a cold wave. The years with greater occurrence of cold waves and frost formation coincide with La Niña events, when changes in the normal atmospheric circulation patterns favor the action

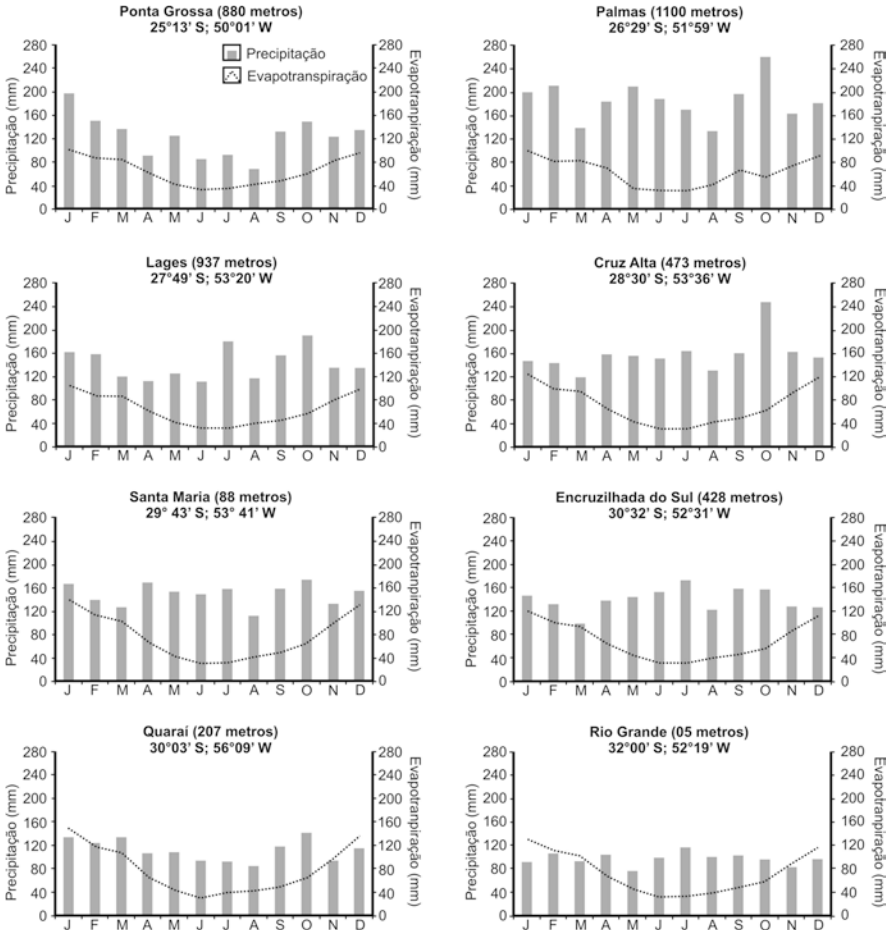

Fig. 6.3 Annual variation of air temperature and accumulation of cold hours (<7.2 °C) in different locations of the South Brazilian grasslands. Upper and lower ends of vertical bars represent the monthly average of absolute maximum and minimum temperatures (°C), respectively. Upper and lower limits of black boxes represent the monthly averages of maximum and minimum temperatures (°C) and gray horizontal bars represent the monthly average temperatures (°C). Total sum of cold hours (<7.2 °C) between May and September are presented at the top of the figure. (Source of climatic data: Wrege et al. 2012)

of polar masses throughout southern Brazil (Aguiar and Mendonça 2004; Berlato and Althaus 2010; Firpo et al. 2012). In contrast, due to the increase in cloudiness, in El Niño years, winters tend to be milder, with a reduction in the occurrence of cold waves, low temperatures and frost formation (Aguiar and Mendonça 2004; Marengo and Camargo 2008; Berlato and Althaus 2010; Firpo et al. 2012).

Studies related to climate change have identified a significant increase in minimum temperatures throughout the southern region of Brazil in the recent past (Vincent et al. 2005; Marengo and Camargo 2008; Berlato and Althaus 2010;

Sansigolo and Kayano 2010). Analyzing a time series of almost 100 years from six locations in southern Rio Grande do Sul, Sansigolo and Kayano (2010) identified an increase in minimum temperatures of more than 1.5 °C for all four seasons. Additionally, there has been a reduction in the annual occurrence of cold waves in southern Brazil over the past six decades (Bitencourt et al. 2020). The trend of increasing minimum temperatures is consistent with the global scenario of climate change related to greenhouse gas emissions and is also recorded in other regions of South America (Vincent et al. 2005). However, in southern Brazil, it may also be associated with the increased frequency and intensity of El Niño events during the late twentieth century and early twenty-first century (Berlato and Althaus 2010; Marengo and Camargo 2008).

Atmospheric circulation also affects maximum temperatures. Most of the absolute records are recorded during episodes of heat waves associated with atmospheric blocks that prevent the advance of polar fronts, causing a succession of dry days and with a large temperature range (Reis et al. 2019). In southern Brazil, heat waves occur mainly from autumn to spring, with most events recorded in winter, and less frequently in the summer months (Firpo et al. 2012; Reis et al. 2019). Heat waves are more frequent in El Niño years (Firpo et al. 2012), with records of them in all years of occurrence of this phenomenon (Reis et al. 2019). The occurrence of days considered exceptionally hot, with daily temperature higher than the average of the historical series maximums, is also usually more frequent in El Niño years (Marengo and Camargo 2008). Contrary to the trend observed for minimum temperatures, studies evaluating climate change in southern Brazil have not verified a consistent pattern for maximum temperatures, with cooling trends during the summer in some locations (Vincent et al. 2005; Marengo and Camargo 2008; Sansigolo and Kayano 2010).

6.2.2.3 Rainfall

In general, the South Brazilian grasslands are under high rainfall and without dry season, although periods of drought or sequences of months with water deficiency are frequent in some regions (Nery et al. 2002; Kulman et al. 2014). The high annual rainfall results from both the contribution of water vapor from local/regional evapotranspiration and moisture from the Atlantic Ocean and tropical areas of Brazil (Grimm 2009a, b; Zemp et al. 2014). The highest accumulations are seen in western region of SC and PR, with more than 2000 mm annually (Wrege et al. 2012), and the lowest along the southern coast of RS, ranging between 1100 and 1200 mm annually (Wrege et al. 2011). In Fig. 6.4, these extremes are represented, respectively, by the localities of Palmas (PR) and Rio Grande (RS). As for the annual distribution in SC and PR, the summer months tend to present the highest accumulations, while in most of Rio Grande do Sul the highest precipitation tends to occur between late winter and early spring (Nimer 1979; Grimm 2009a, b).

Throughout the year, rainfall in the southern region of Brazil is influenced by different atmospheric systems. During fall and winter, the South Atlantic

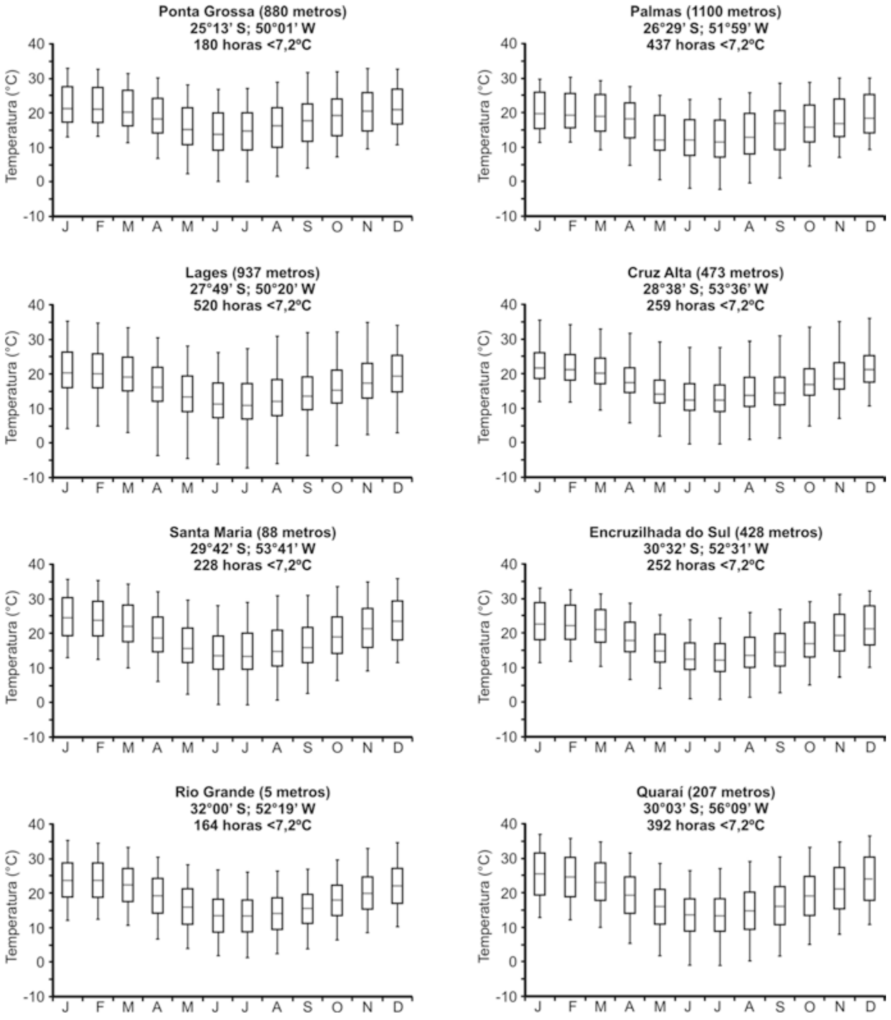

Fig. 6.4 Annual variation of rainfall and potential evapotranspiration at different locations in the South Brazilian grasslands. Gray bars represent monthly average rainfall (mm) and black dashed lines represent monthly average potential evapotranspiration (mm). Cumulative annual totals are shown at the top of the graphs. (Source of climatic data: Wrege et al. 2012)

anticyclone (also known as the Saint Helena anticyclone) is strengthened and positioned near the Brazilian coast at the latitude of the Tropic of Capricorn (23° 27′ S), creating a flow of warm and humid air from east to west that invades the continent at tropical latitudes (Nimer 1979). When it arrives in central South America, this air flow reverses its direction to the southeast, becoming the predominant circulation and the main source of moisture that reaches the southern region of Brazil from May through September (Grimm 2009a, b). Although it contains a large amount of moisture, coming from ocean evaporation and evapotranspiration from tropical areas in Brazil, the subsidence nature of this atmospheric system tends to generate weather stability throughout southern Brazil. This stability is usually reduced by the occasional passage of two other types of atmospheric systems, the mobile anticyclones and the extratropical cyclones.

The mobile anticyclones detach from the Atlantic Polar Mass in the high latitudes of the Southern Hemisphere and head toward the tropical region, following a southwest to northeast trajectory (Cavalcanti and Kousky 2009). When a mobile anticyclone reaches southern Brazil, it comes into contact with the tropical air mass that was acting in the region until then. In this contact, the cold dense air from the anticyclone advances over the surface, lifting the less dense (hot and humid) tropical air, leading to its cooling and to the condensation of water vapor, forming lines of instability hundreds of kilometers long (Nimer 1979). The passage of these fronts usually results in prolonged frontal rains covering a large extension, followed by very cold and dry days (see previous section). Extratropical cyclones form mainly on the southeast coast of Argentina (40–55°S), and less frequently in the continental area near the mouth of the La Plata River (35°S) and on the coast of the southern region of Brazil (30°S) (Gramcianinov et al. 2019). These systems have an average life span of 3–4 days, and their passage on the coast of southern Brazil usually causes heavy rainfall, wind-, and ocean storms (Rocha et al. 2016). While the passage of polar fronts tends to affect almost homogeneously the South Brazilian grasslands and other areas of central South America, extratropical cyclones usually have their effects restricted to the coastal areas of southern Brazil.

During the spring and summer months, the higher incidence of solar radiation results in a progressive warming of the Southern Hemisphere and the consequent weakening of the South Atlantic anticyclone, which moves to a more southerly position (28°S) and further away from the South American continent (Grimm et al. 1998). This displacement generates prevailing NE winds near the coast of the southern region of Brazil, bringing moisture from the ocean to the coastal areas and favoring the occurrence of convective rains in some areas in the eastern part of the South Brazilian grasslands (Hasenack and Ferraro 1989). Additionally, the weakening and displacement of the South Atlantic anticyclone also allows the penetration of a greater amount of moisture in the center of South America, leading to an increase in the convective process and greater atmospheric instability in much of the Brazilian territory (Grimm 2009a, b).

During this period, the transfer of moisture from the tropical region to southern Brazil occurs mainly by the air flow known as the South American Low-Level Jet. This flow of moist air originates in the trade winds of the Tropical Atlantic, which blow from east to west and cross the entire length of the Amazon plains, being subsequently deflected southward when they meet the physical barrier of the Andes Mountains (Marengo et al. 2002). From there, this flow moves at low altitude (1–2 km above sea level) at an average speed of 30 km/h up to latitudes 25–35°S, and is responsible for much of the moisture that forms the clouds and precipitation in the La Plata River basin during the summer, which includes much of the western portion of the South Brazilian grasslands (Arraut et al. 2012). The moisture transported by the South American low altitude jet also reaches the southeast region of

Brazil (Marengo et al. 2002), where it intensifies the action of the South Atlantic Convergence Zone (ZACA) and mesoscale convective systems (Grimm 2009a). Depending on its latitudinal displacement, the ZACA can influence the precipitation in the northern part of the South Brazilian grasslands, which explains, at least in part, the higher volume of rainfall during the summer at locations in the state of Paraná (Grimm 2009a).

In contrast to temperature, relief has little effect on the distribution and volume of rainfall in the South Brazilian grasslands. Its influence is mostly restricted to the eastern edge of the South Brazilian Highland (see Fig. 6.5) and the areas on the slopes facing the Atlantic Ocean. Especially in spring and summer months, the humid wind from the South Atlantic anticyclone, which flows from the ocean to the continent, rises over these slopes and cools, generating condensation, fog and orographic rains that usually occur in the afternoon (Grimm 2009a). This phenomenon is evidenced in several locations in the highlands in northeastern RS (municipalities of São Francisco de Paula, Cambará do Sul, and São José dos Ausentes) and southeastern SC (municipalities of São Joaquim and Urubici), making this region one of the wettest of the South Brazilian grasslands. Historically, these areas also record the highest frequency of snow precipitation across Brazil (Schmitz 2007).

Teleconnection events significantly affect precipitation over the entire length of the South Brazilian grasslands, with the effects caused by ENSO events the best documented to date. During El Niño events, annual precipitation at different locations in the southern region of Brazil tends to be well above the historical average, with an opposite trend in years of La Niña occurrence (Grimm 2009b). In both situations, the most pronounced effects are registered during spring, with November being the month of greatest variation in precipitation (Grimm et al. 1998). Using the whole set of available data from 29 meteorological stations in Rio Grande do Sul, with series ranging from 48 to 82 years of observation, Fontana and Berlato (1997) quantified the rainfall deviations of ENSO events from the historical average of these locations for the months of October and November. During El Niño events, the average increase in precipitation in the north of the state (40–70 mm) was greater than that observed in the south (30–40 mm). In contrast, during La Niña years, the reduction in rainfall showed an increasing gradient from east to west, with reductions ranging from 80 mm in coastal areas to 120 mm in the far west of Rio Grande do Sul (Fontana and Berlato 1997).

However, what ratifies the susceptibility of the region to changes in the general atmospheric circulation patterns are the records of the most intense ENSO events. The 1924 drought, caused by a La Niña event, is considered the most intense negative anomaly that occurred in the twentieth century, having impacted the southern region of Brazil with reductions ranging from 300 to 900 mm in annual rainfall (Nimer 1979; Valente 2018). On the other hand, between October 1997 and May 1998, different places in southern Brazil received, on average, 50 mm/month higher rainfall than their historical averages, in what is internationally recognized as the

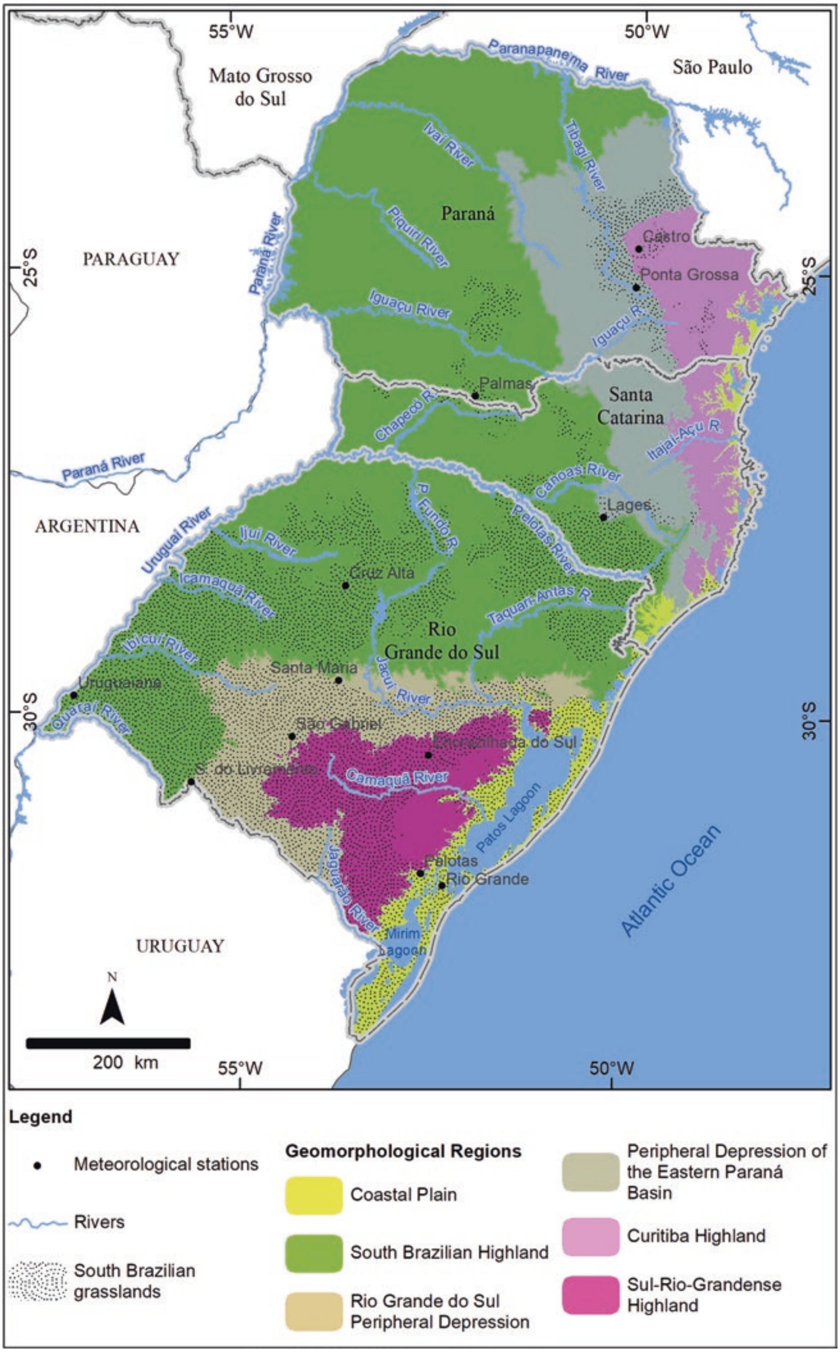

Fig. 6.5 Geomorphological regionalization of the South Brazilian grasslands, with indication of the potential distribution of grasslands.

most intense El Niño recorded until the end of the twentieth century (Oliveira and Satyamurty 1998).

ENSO is not the only mode of climate variability capable of producing significant changes in rainfall in the South Brazilian grassland regions. During the negative phase of the Southern Hemisphere Annular Mode (SAM), there is a weakening of the westerly winds in the southern hemisphere, leading to an increase in the frequency of front formation in southeastern South America and a northward migration of extratropical cyclones (Reboita et al. 2009). Thus, when the negative phase of SAM is active, positive rainfall anomalies tend to be recorded across the southern region of Brazil during autumn and spring, with more pronounced deviations occurring in southern Rio Grande do Sul (Carpenedo and Ambrizzi 2020). During the positive SAM phase, these conditions reverse, and the South Atlantic anticyclone moves to a more southerly position than usual, favoring meteorological stability. In this scenario, all of southern Brazil tends to record below-average precipitation during spring, although this trend can also be observed during part of fall and summer on the coast and in southern RS (Schossler et al. 2018; Carpenedo and Ambrizzi 2020). Simulations of the general circulation show that the SAM has been in a positive phase trend since the late 1950s (Marshall 2003).

Regarding climate change, some studies suggested a trend of increased rainfall in the southern region of Brazil (Sansigolo and Kayano 2010; Pinheiro et al. 2013; Ávila et al. 2016; Berlato and Cordeiro 2018). However, most greenhouse gas emissions scenarios in model simulations for the future have projected profound changes in ocean surface temperature and atmospheric circulation in the Pacific Ocean region, leading to increased frequency of extreme El Niño (Cai et al. 2014) and La Niña (Cai et al. 2015) events. Recently, Valente (2018) observed a trend of intensifying El Niño and La Niña effects for southern Brazil, where even events considered weak or moderate in the Pacific Ocean caused significant impacts on precipitation in the region. Other anthropic factors can also lead to changes in the rainfall regime of the South Brazilian grasslands. Recent increases in deforestation and the number of wildfires in the Amazon and Cerrado, for example, may lead to a weakening of the South American low altitude jet, which would decrease water vapor transport relevant for summer rainfall in Southern Brazil (Zemp et al. 2014; Thornhill et al. 2018). Therefore, from the scenarios presented, it is likely that in the coming decades the South Brazilian grasslands will experience a higher frequency of extreme events, with alternation of exceptionally rainy periods and severe droughts (Marengo 2009; Schossler et al. 2018).

6.2.2.4 Evapotranspiration

Although rainfall is high throughout the year in the South Brazilian grasslands, episodes of water deficiency can occur in drier years. Unfortunately, the official weather station network does not have lysimeters to measure evapotranspiration, even though this is an essential variable for calculating the climatological water balance. For this reason, Fig. 6.4 illustrates an estimate of potential evapotranspiration, which corresponds to the maximum loss of water vapor to the atmosphere by a growing vegetation completely covering a horizontal surface and fully exposed to atmospheric conditions, without soil water restriction (Tubelis and Nascimento 1988).

The highest annual potential evapotranspiration rates in the South Brazilian grasslands are seen in the far west of RS (>900 mm), while the lowest are registered in the grasslands in the higher elevations of the South Brazilian highland (<700 mm) (Wrege et al. 2011). The difference is mainly due to the higher evaporative demand of the atmosphere in the South and West of RS in the summer months, due to higher temperatures (Leivas et al. 2006). In the highlands, besides the milder temperatures, the location closer to the Atlantic Ocean also provides additional humidity. During winter, the southernmost region of South Brazil have a greater reduction in the photoperiod and in the amount of incident solar radiation. Thus, between June and August, locations in PR have a slightly higher potential evapotranspiration than those in the far west of RS (Wrege et al. 2012).

In the far west of RS, in the region bordering Uruguay, the historical monthly average of potential evapotranspiration rates can exceed that of the rainfall during the summer, as in the case of Quaraí (Fig. 6.4). In this case, depending on the water storage capacity in the soil, there can be a more or less pronounced water deficit. The extreme west and the border with Uruguay are the areas most prone to the occurrence of water deficit in Rio Grande do Sul, especially between the months of December and January (Leivas et al. 2006). Historically, these two regions are also the ones that most frequently experience the socioeconomic impacts resulting from it, such as losses in the agricultural sector and water shortages for the population. In the South Brazilian grasslands, the water deficit during summer is more frequent in La Niña events (Kulman et al. 2014; Brondani et al. 2013).

6.3 Characteristics of the Soils

6.3.1 The Geological-Geomorphological Context

In the South Brazilian grassland region, the highlands are represented by the Curitiba Highland, the Sul-Rio-Grandense Highland and the South Brazilian Highland, which occur over two distinct morphostructures (Ross 2006) (Fig. 6.5). The first two are associated with the orogenic belt of the Mantiqueira Province, a crystalline basement whose formation occurred between 950 Million years ago (Ma) of the Neoproterozoic period, Proterozoic Era, up to the Cambrian period, Paleozoic Era), while the South Brazilian Highland associated with rocks resulting from a fissure volcanism that deposited numerous layers of mafic and felsic rocks over the sedimentary basin of the Paraná River, mainly between 145 and 66 Ma, in the late Jurassic and Cretaceous period, Mesozoic Era (Bizzi et al. 2003, see also Menegat 2023, Chap. 2 in this volume).

Between these highlands lie the peripheral foreland basins Depression of the Eastern Paraná Basin in the states of Paraná and Santa Catarina and the Rio-Grande-do-Sul Depression in the state of Rio Grande do Sul. Both are part of the large sedimentary basin, the Paraná Basin that was formed along the Cambrian, Paleozoic Era, up to the Jurassic, Mesozoic Era (between 540 Ma and 145 Ma) as a result of colluvial material eroded from the crystalline basement whose sediments where reworked by glacial, fluvial, and aeolian processes. The peripheral depressions correspond to the portions of the Paraná Basin not covered by the basaltic flows of the late Mesozoic Era. The Coastal Plain formed during the Quaternary period of the Cenozoic era (between 400 ka and 5 ka), from fluvio-lagoon and marine sediments deposited after a sequence of four transgressive-regressive sea-level events (Tomazelli et al. 2000).

Soils are located at the interface between the earth's crust and the atmosphere and their formation is the result of the combined action of different forming factors. Tectonic movements and the action of climate on the parent material have, over time, created diverse landforms allowing the formation of different types of soil, also with the contribution of organisms.

6.3.2 Main Soil Groups

Because of the diversity of soils in the region, here we analyze only the mapping units of soils located within the grassland areas. We grouped the soils in relation to the geomorphological units described above, relative to the first two taxa: the morphostructures that constitute the geological foundation and the morpho-sculptures, the forms resulting from the action of the climate (Ross 2006).

To facilitate the relationship between soils and grassland vegetation, we performed a reclassification of soil map units into functional classes based on properties relevant to grassland vegetation development at a regional scale. To this end, we used the information contained in the best-detailed soil survey available for the region, including a 1:250,000 scale map and analytical and descriptive data of representative profiles (IBGE 2018) and grouped them into four functional categories, considering the properties of the dominant soil class in each map unit (Hasenack et al. 2023): (1) deep soils with high fertility, (2) deep soils with low fertility, (3) shallow soils, and (4) hydromorphic soils (Table 6.1). These classes in turn were regionally described considering the geomorphological regions where these soils occur in the South Brazilian grasslands (Fig. 6.5). Soil nomenclature follows the Brazilian System of Soil Classification (SiBCS) (EMBRAPA 2018), and corresponding classes of the FAO Soil Classification System (IUSS Working Group WRB 2015) and the Soil Taxonomy (Soil Survey Staff 1999) are indicated in Table 6.1.

6.3.2.1 Soils in Highlands Associated to the Crystalline Basement

On the **Curitiba Highland**, located in the eastern part of PR, the Curitiba-Castro grassland occurs at elevations about 900 m, where gentle slopes dominate. In these areas, deep soils with low fertility predominate, represented mainly by *Latossolos Vermelho-Amarelos Distróficos*. To a lesser extent, *Argissolos Vermelho-Amarelos alumínicos* and *Cambissolos Háplicos alumínicos* can also be found. With less expression, hydromorphic soils are present along the watercourses, represented by *Organossolos Háplicos flúvicos*.

On the **Sul-Rio-Grandense Highland**, located in the southeastern portion of the state of Rio Grande do Sul, the Shrub Grassland (Fig. 6.1) is distributed at elevations lower than those of the Curitiba Highland, reaching just over 500 m, with undulating to strong undulating relief. The highland is very dissected and the mountains and hills have rounded tops. The complex geological structure of this

Table 6.1 Soils occurring in the South Brazilian grasslands, their classification in the Brazilian System of Soil Classification (SiBCS) (EMBRAPA, 2018) and respective correspondence to the FAO Soil Classification System (FAO/WRB) (IUSS Working Group WRB 2015) and to the US Soil Classification System (Soil Taxonomy) (Soil Survey Staff 1999)

Geomorphological regions	Grassland ecological system	Functional soil class	Soil SiBCS	Soil FAO/WRB	Soil Taxonomy
Soils in highlands associated to the crystalline basement	Curitiba-Castro Grassland	Deep soils with low fertility	Latossolos Vermelho-Amarelos Distróficos	Dystric Ferralsol	Udult
			Argissolos Vermelho-Amarelos alumínicos	Haplic Acrisol	Udult
			Cambissolos Háplicos alumínicos	Dystric Cambisol	Umbrept
		Hydromorphic soils	Organossolos Háplicos flúvicos	Histosol	Histosol
	Shrub Grassland	Deep soils with low fertility	Argissolos Vermelho-Amarelos Distróficos	Haplic Alisol	Typic Paleudult
		Shallow soils	Neossolos Litólicos distróficos e eutróficos	Lithic Leptosol	Ustorthent

(continued)

Table 6.1 (continued)

Geomorphological regions	Grassland ecological system	Functional soil class	Soil SiBCS	Soil FAO/ WRB	Soil Taxonomy
Soils in highlands on sedimentary basins (peripheral foreland basins) – Meridional Highland	Guarapuava-Palmas Grassland	Deep soils with low fertility	Latossolos Brunos alumínicos	Humic Ferralsol	Humic Haploperox
			Cambissolos Alumínicos húmicos	Humic Cambisol	Umbrept
	Lages-Vacaria Grassland	Deep soils with low fertility	Cambissolos Aluminicos húmicos	Humic Cambisol	Umbrept
			Latossolos Vermelhos aluminoférricos	Rhodic Ferralsol	Humic Haploperox
	Aristida Grassland	Deep soils with low fertility	Latossolos Vermelhos distróficos	Dystric Ferralsol	Ustox
		Shallow soils	Neossolos Litólicos chernossólicos	Lithic Leptosol	Udorthent
	Park Grassland	Deep soils with high fertility	Nitossolos Vermelhos eutróficos	Rhodic Nitisol	Udox
			Chernossolos Ebânicos carbonáticos	Luvic Phaeozem	Udoll
		Hydromorphic soils	Plintossolos Argilúvicos distróficos	Dystric Plinthosol	Plintaquults
	Shallow Soil Grassland	Shallow soils	Neossolos Litólicos chernossólicos	Lithic Leptosol	Udorthent
	Sandy Grassland	Deep soils with low fertility	Latossolos Vermelhos distróficos	Haplic Dystric Ferralsol	Udox; Ustox
		Deep soils with low fertility	Neossolos Quartzarênicos órticos	Ferralic Arenosol	Quartzipsamment

Table 6.1 (continued)

Geomorphological regions	Grassland ecological system	Functional soil class	Soil SiBCS	Soil FAO/WRB	Soil Taxonomy
Soils on shaped depressions at the border of sedimentary basins	Ponta Grossa-Tibagi Grassland	Deep soils with low fertility	Latossolos Vermelho-Amarelos distróficos	Dystric Ferralsol	Ustox
			Cambissolos Húmicos alumínicos	Dystric Cambisol	Umbrept
			Cambissolos Háplicos alumínicos	Dystric Cambisol	Ochrept
	Inland Sub-montane, Atlantic Sub-montane, and Short Grass Grasslands	Deep soils with low fertility	Argissolos Vermelhos alumínicos	Haplic Acrisol	Ultisol
		Deep soils with high fertility	Luvissolos Háplicos órticos	Haplic Luvisol	Udalf
			Chernossolos Ebânicos carbonáticos	Haplic Phaeozem	Albaqualfs
		Hydromorphic soils	Planossolos Háplicos eutróficos	Eutric Planosols	Albaqualfs
Soils of coastal plains and terraces	Coastal plain	Hydromorphic soils	Planossolos Háplicos eutróficos	Eutric Planosols	Albaqualfs
			Gleissolos Háplicos Ta eutróficos	Eutric Gleysols	Aqualfs
			Gleissolos Melânicos Ta eutróficos	Mollic Gleysols	Aquents
			Plintossolos Háplicos alumínicos	Plinthosol	Plintaquults
			Neossolos Quartazarênicos hidromórficos	Dystric Fluvisol	Fluvent

crystalline shield, shaped by different climatic conditions for at least 140 Ma, has produced a great variety of topographic conditions, resulting in a high diversity of soil types. In this region, deep soils with low fertility and shallow soils in similar proportions dominate in the grassland areas. The former are predominantly represented by *Argissolos Vermelho-Amarelos distróficos*, while the shallow soils are mainly represented by *Neossolos Litólicos distróficos e eutrófico*s, in equal proportions.

6.3.2.2 Soils in Highlands on Sedimentary Basins (Peripheral Foreland Basins)

The **South Brazilian Highland**, formed after a sequence of volcanic fissural outpouring of mafic and felsic rocks, has a flat top in the form of a cuesta with highest elevation in the East. In this region, it reaches an altitude of 1500 m in Bom Jardim da Serra (SC) and 1200 m in Palmas (PR) and in São José dos Ausentes (RS), at the contact with the cuesta front. The altitude gradually decreases toward the interior of the continent until it reaches about 100 m in the extreme west, close to the Paraná river in the north and the Uruguay river in the south. The grasslands occur on the top of the highland, where the slopes are gentle to undulating. Due to the latitudinal extent and elevation range of the highland, the soil description was regionalized according to the distribution of grassland areas in this geomorphological region:

The **Guarapuava-Palmas Grassland** is located in the mid-southern region of the state of PR, and partially extends also into the mid-north region of neighbor state of SC. The grassland vegetation occurs at elevations between 1100 and 1200 m in Guarapuava and Palmas (PR), and around 900 m in Campo-Erê (SC), where the relief is gentle to undulating. The predominant soils in these grassland areas are deep and with low fertility, represented mainly by *Latossolos Brunos alumínico*s e *Cambissolos Alumínicos húmicos*, in an approximate ratio of 2:1.

In the **Lages-Vacaria Grassland**, located in the southeast of the state of Santa Catarina and northeast of the state of Rio Grande do Sul, the elevations range from 1500 m in Bom Jardim da Serra in the east, decrease to 900 m in Lages (both in the state of Santa Catarina) and Vacaria (state of Rio Grande do Sul), reaching 600 m in Passo Fundo and Soledade (state of Rio Grande do Sul) in the southwest. Throughout this region, grassland vegetation occurs at the top of the highland on gently to undulating terrain, where deep soils with low fertility predominate, represented by *Cambissolos Alumínicos húmicos* e *Latossolos Vermelhos aluminoférricos*.

For the northwestern and western portion of the South-Brazilian Highland, in RS, Hasenack et al. (2023) described four distinct ecological systems: the *Aristida* Grassland, the Park Grassland, the Sandy Grassland, and the Shallow Soils Grassland:

The **Aristida Grassland**, named by the grass genus *Aristida* whose species are a conspicuous element of these grasslands, is located in the Northwest of RS and comprises a region in which elevations of the top of the highland vary from 600 m, in Palmeira das Missões, to about 200 m in São Miguel das Missões and reach a little less than 100 m near the Uruguay River, in São Borja, at the border with Argentina. The dominant soils are predominantly deep with low fertility, especially the Latossolos Vermelhos distróficos, with minor occurrence of shallow soils, especially the Neossolos Litólicos chernossólicos.

The **Park Grassland** is located along the Uruguay river, at the border with Argentina at the far west between São Borja and Uruguaiana. Elevation rarely exceeds 100 m and slopes are gentle to undulating. Places with gentle slopes and where the water table is close to the surface favor the occurrence of wetlands and swamps. This condition, associated with high temperatures, favors weathering. This is probably the reason for the low altitude of the region, and for the almost total weathering of the basaltic flows in this grassland region. Deep soils with high fertility predominate in the region, represented in greater proportion by Nitossolos Vermelhos eutróficos and *Chernossolos Ebânicos carbonáticos*. The second functional category present in this region corresponds to hydromorphic soils, whose largest coverage in area corresponds to *Plintossolos Argilúvicos distróficos*.

The **Sandy Grassland** is located upstream of the Park Grassland in places where the thin layer of the first volcanic fissure spills was weathered to create deep soils with low fertility, here dominated by the *Latossolos Vermelhos distróficos*. In some areas where these soils have been eroded, underlying unconsolidated sandy sediments, locally called "areais" are exposed. Slopes are gentle and elevation lies between 100 and 200 m. On these sandy surfaces, *Neossolos Quartzarênicos órticos* were formed, which occur in a smaller proportion in the soil map units because they are mostly smaller patches included in the mapping units of the region in which the *Latossolos Vermelhos distróficos* predominate.

The **Shallow Soil Grassland** is located in the southwest of the state of Rio Grande do Sul, where elevations range from about 250 m in the East, near the city of Santana do Livramento, to less than 100 m in Uruguaiana and Barra do Quaraí in the West. In this region, the grasslands occur on gentle slopes and shallow soils, represented mainly by *Neossolos Litólicos chernossólicos*. Although the rainfall is distributed throughout the year and the soils have high natural fertility, the vegetation ends up being subjected to a water deficit due to the low water retention capacity since the soils are shallow.

6.3.2.3 Soils on Shaped Depressions at the Border of Sedimentary Basins

The **Peripheral Depression of the Eastern Paraná Basin** corresponds to colluvial and alluvial deposits of the crystalline origenic belt in the east of the states PR and SC. These deposits date back to the Paleozoic era and have since then been reworked and correspond to the uncovered part of the volcanic fissure spills that formed the highland of the Paraná Basin. In this Peripheral Depression, grasslands occur at elevations around 800–1000 m, on slopes varying from gentle to undulating. The Ponta Grossa-Tibagi grassland is found on deep soils with low fertility, the most frequent being the *Latossolos Vermelho-Amarelos distróficos*, the *Cambissolos Húmicos alumínicos,* and the *Cambissolos Háplicos alumínico*s.

The **Rio-Grande-do-Sul Peripheral Depression** is composed of Paleozoic sediments from the weathering of the Sul-Rio-Grandense Highland, whose colluvial material was deposited in its surroundings, and later covered by layers of glacial, fluvial, deltaic, marine, and eolic sediments, subsequently reworked by the action of wind, water, and the variation of high and low temperatures since the Paleozoic era. This Peripheral Depression surrounds the Sul-Rio-Grandense Highland from the north, the west to the southwest, separating it from the South Brazilian Highland. Different from the Peripheral Depression of the Eastern Paraná-Basin, however, the Rio-Grande-do-Sul Peripheral Depression has much lower elevations, between 30 and 100 m, and the slopes vary from gentle to undulating. The source material and the fact that the water table is close to the surface, in addition to its position in relation to the neighboring highlands, lead to a wide variety of soils, even considering small altimetric variations. The soils in contact with the highlands contain a greater proportion of colluvial material and, because they are at a higher position within the Depression, tend to be better drained. The areas near the regional base level, on the other hand, in addition to the lower altitude, present greater hydromorphism as a result of the water table being close to the surface (Streck et al. 2018). Based on this altimetric gradient within the Depression, at higher and better drained places the *Argissolos* and *Plintossolos* are more frequent, and on imperfectly drained places the *Planossolos*, *Luvissolos*, *Chernossolos*, and *Vertissolos*. The *Gleissolos* occur along the drainage and in poorly drained areas.

The grasslands of this region are classified into the Atlantic Submontane Grassland, the Interior Submontane Grassland, and the Shortgrass Grassland (Hasenack et al. 2023; Fig. 6.1). Throughout these systems, deep soils with low fertility dominate, represented mainly by *Argissolos Vermelhos alumínicos*. In the rest of the area, deep soils with high fertility and hydromorphic ones occur in similar proportions. Among the former are *Luvissolos Háplicos órticos* and *Chernossolos Ebânicos carbonáticos*, while most of the hydromorphic soils are represented by *Planossolos Háplicos eutróficos*. Some soils, such as the *Argissolos*, the *Planossolos,* and the *Gleissolos*, are widely distributed in the Peripheral Depression of Rio Grande do Sul, while others have a more regionalized occurrence, such as the *Luvissolos* and the *Chernossolos*. The high fertility of soils, associated with a milder climate when compared to other areas where grassland vegetation occurs in southern Brazil, especially favors the coexistence of both summer and winter species (in particular C4 and C3 grasses; see Chap. 3), which is typical for South Brazilian grasslands.

6.3.2.4 Soils of Coastal Plains and Terraces

The **Coastal plain** was formed during the Quaternary Period, Cenozoic Era (between 400 ka and 5 ka), when a succession of four transgressive-regressive periods resulted in a sequence of sandy barriers parallel to the coast interspersed with sandy depressions, but humid, in which even today one can find lagoons and wetlands (see Menegat 2023, Chap. 2). This landscape is most characteristic along the entire coast of Rio Grande do Sul, where it reaches a width of 100 km, and in the southeastern coast Santa Catarina, up to the municipality of Laguna. Here, it forms a continuous plain that contains large lagoons and numerous lakes, including the Patos Lagoon and Mirim Lagoon, whose formation began with the first barrier, and many lakes lined up like a rosary between the third and fourth barriers. From Laguna northward, until the border between the states of Paraná and São Paulo, the plains are established between the rocky spurs by the sea, forming inlets of different extensions.

The elevations are below 30 m, and the predominant slope is flat, with the occurrence of essentially sandy soils. The proximity to sea level causes the water table to be close to the surface, so that small altimetric differences are sufficient to define two extremes: well-drained soils in the higher portions and imperfectly or poorly drained soils in the lower portions, near swamps or around water bodies.

Hydromorphic soils dominate the Coastal Grassland, where *Planossolos Háplicos eutróficos* are the most frequent, found in about one third of the area. *Gleissolos Háplicos Ta eutróficos* are also found, occupying about 15% of the area, and Gleissolos Melânicos Ta eutróficos, with about 10%. In the remaining areas are found in similar proportions *Plintossolos Háplicos* alumínicos e *Neossolos Quartazarênicos hidromórficos*. From the standpoint of their position in the landscape, *Plintossolos* and *Planossolos* are found in slightly higher portions, such as terraces, while *Gleissolos* occur near water bodies and swamps. *Neossolos Quartzarênicos* and dunes occur in the barriers closer to the sea.

6.4 Final Considerations

Our characterization of soil and climate indicates that the South Brazilian grassland region is highly variable in regard to climatic and edaphic conditions, which relates to a variety of grassland systems that are only started to be described in more detail (Andrade et al. 2019) and, together also with historical processes and biogeographic patterns, provides the basis for the high biodiversity found in the region (e.g. Andrade et al. 2023). Grasslands occur predominantly on gentle to undulating relief, except in the Sul-Rio-Grandense Highland, where the grasslands also occur on strongly undulating relief, and are present in all functional soil classes. However, the in general very favorable conditions for vegetation development in the region also mean diverse possibilities for cultivation of a large variety of domestic plants, in different production systems. In consequence, the South Brazilian grasslands region has seen, and still is seeing, fast changes in land use and land cover (see for example Cordeiro & Hasenack 2009; Baeza et al. 2022; Gallego et al. 2023, Chap. 18, this Volume), with strong regional differences due to natural conditions (in particular, topography and soils), but also colonization and land use history.

Over the last decades, the southern region of Brazil has been registering a trend of increasing annual average temperature around 0.56 °C (Aquino 2012). This regional warming trend occurs mainly by the increase in minimum/nighttime temperatures that is more pronounced than increase in maximum/daytime temperatures (Vincent et al. 2005; Sansigolo and Kayano 2010; INMET 2022; Hofmann et al. 2023). Further, an annual trend of increasing precipitation has been observed (Hofmann et al. 2023). This pattern is in line with the global scenario of climate change due to the increasing concentration of greenhouse gasses in the atmosphere and can also be observed in other regions of South America and the world. Specifically in the southern region of Brazil, warming may also be associated with changes in the normal atmospheric circulation patterns induced by teleconnection events, such as the intensification of ENSO and the maintenance of the positive phase of SAM (Marengo and Camargo 2008; Aquino 2012). These changes will affect dynamics of natural vegetation, possibly accelerating the trend of forest expansion over grasslands observed in the region over the past millennia (see Behling et al. 2023, this volume). However, as large parts of the region are now used for agriculture, including grazing lands, agricultural fields, and tree plantations, severe effects can also be expected on agricultural production, as already observed during dry spells in the past years. Likely, these changes will provide considerable challenges for land use in the region. Grasslands itself certainly will also change in composition as species distribution patterns change, and in response to anthropogenic drivers such as management intensification, fragmentation, or invasion of exotic species. However, the fact that grasslands naturally occur across great long edaphic and climatic gradients may facilitate their adaptation to future climate change.

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Chapter 7
The Southern Grasslands and the Expropriation of Indigenous Territories

Tau Golin

7.1 Introduction

Before the Treaty of Madrid (1750), the Southern Grasslands belonged exclusively to the indigenous peoples who either autonomously occupied the region or were associated with the Society of Jesus. They were organized into three major groups: Pampean, Jê, and Guarani, each encompassing distinct ethnicities or "nations". The Treaties of Madrid and Saint Ildefonso, geopolitically endorsed by Portugal and Spain, established dividing lines traversing indigenous land. The resulting borders became sites of interethnic friction and conflicts with the colonizers, escalating into violent settings characterized by banditry, robbery, extermination, and occupation.

During the land demarcation period of the Treaty of Madrid (1752–1761), the territory was shared by various Pampean nations, notably the Guenoa-Minuano, Yaro, Bohane, and the traditional Guarani and the *missioneiro* Guarani.[1] There were also other groups associated with the Charrua, which were primarily settled between the Paraná and Uruguay Rivers. The Pampean people would assert territorial control

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[1] *Missioneiro*: In Portuguese, there is an important distinction between the terms "*missioneiros*" and "*missionários*," which translates as *missionaries*. While both terms refer to individuals associated with the missions, they represent different groups with distinct roles and backgrounds. "*Missionários*" refers to the Christian missionaries, typically European priests, who were members of religious orders such as the Jesuits, Franciscans, or Dominicans. Their primary role was spreading Christianity and establishing and managing the mission settlements or reductions. On the other hand, "*missioneiros*" refers specifically to the indigenous inhabitants of the missions, who were converted to Christianity and lived within these missionary communities.

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by building villages comprising *toldarias*,[2] *rancherios*,[3] and areas dedicated to raising their herds of cattle, mules, and horses. In specific locations, they established strongholds within and between *missioneiro* estates that extended from the Uruguay River to the Quaraí, Alto Rio Negro, Alto Camaquã, and Jacuí Rivers. These settlements were maintained by large families led by tribal chiefs and were engaged in herding and cultivating crops of corn, yuca, potatoes, sugar cane, vegetables, and orchards. They developed the production of grease, tallow, hides, horn tools, harnesses, and cotton and wool weaving. Their grounds were often characterized by the presence of peach trees ("*duraznal*") brought from China by the Jesuits. The headquarters of the *missioneiro* estates functioned as villages, many of which eventually evolved into present-day cities. These communities were organized around an administrative building, which housed the priest, visiting brothers, and cabildo authorities during their periodic inspections. The settlements featured chapels, sheds, stone walls, wintering grounds, posts, and *rancherios*, sometimes accommodating over 100 nuclear families. In Santa Tecla, a large estate in San Miguel, they constructed a *missioneiro*-style building with wall partitions for couples and their children.

In the first few decades of the nineteenth century, the Pampean people significantly declined, with only the Minuano and Charrua remaining. They became increasingly isolated within the Ibirapuitã basin, primarily inhabiting the hilly regions near the springs and along the Quaraí River. On the other hand, the *missioneiros* had their seven cities (Misiones Orientales), various estates, and yerba mate plantations invaded and occupied in 1801 by Portuguese troops (Camargo 2001). During the Cisplatin War (1825–1828), Fructuoso Rivera orchestrated a major *missioneiro* exodus, relocating the remaining communities to settlements in the north-northwest of where Uruguay is now, ultimately completing the degradation of indigenous assets. The surviving indigenous nations transitioned back into small settlements, where they engaged in farming, gathering, hunting, and fishing. Some communities maintained small herds for subsistence as they were forcibly displaced from their cities, ranches, and yerba mate plantations by the Nation-State.

7.2 Permanent Twilight of an Ethnocidal Memory

Written and cartographical documents, often endorsed by governments, institutions, and explorers, evoke strong memories of the territory loss and devastation experienced by the indigenous peoples, including the impact on future generations through impoverishment and the intermixing, leading to new gentilic identities. As we delve into this complex matter, it is crucial to highlight that one of the main issues

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[2] *Toldaria*: traditional tents or dwellings used by the Minuano indigenous people to assemble their villages. These were portable structures made from various materials, such as animal skins, hides, or fabric, designed to be easily assembled and disassembled.

[3] *Rancherio*: small rural villages, indigenous settlements.

concerning indigenous territoriality, aside from intertribal conflicts, revolved around the dichotomy between chieftainships that embraced Catholicism (for various reasons) and those who fought to preserve their heritage and traditional ways of life, which the Iberian deemed as unfaithful ("infidels"). Those who converted and assimilated into the State's immanence began participating in the European spheres of influence. They obtained recognition of their lands, albeit burdened by high taxation and the obligation to accommodate military presence for patrols and warfare against "infidels" and other European adversaries during border conflicts.

For the non-converted indigenous populations, the options were either aligning with "Christian natives" as the *missioneiros* did, aligning with colonial authorities, or choosing isolation, even though these choices were subject to change based on circumstances. This harsh reality impacted the indigenous nations profoundly, particularly the Pampean people who inhabited the Southern Grasslands. Over time, their collective identity eroded, they merged with the broader South American population, and, eventually, their distinct heritage became extinct through intermixing, despite remnants of their traditions and beliefs persisting.

During the seventeenth and eighteenth centuries, significant conversions and interactions occurred between indigenous groups and religious orders, especially the Society of Jesus. These conversions resulted in the indigenous populations becoming subjects of the Spanish Crown, paying tribute, and gradually forming military societies equipped with firearms and traditional military training. However, they maintained connections and alliances with non-converted groups. Historically, these indigenous troops were responsible for resisting and fighting against the *bandeirantes*,[4] Portuguese-Brazilian expeditions, and indigenous shamans/chiefs who rebelled against Christianity.

In the seventeenth century, the *bandeirantes* became the missioneiros' primary adversaries. They would destroy villages of Christian natives and traditional communities, with the sole purpose of raiding and capturing people and taking them to Brazil as slaves. The non-converted groups resisted Christian pressures to convert and retain control over their territories. Despite the tensions, there were alliances between the converted and non-converted populations in various regions. For example, *missioneiros* coexisted, traded, and formed war alliances with the Guenoa-Minuano people, including many Charrua groups in the Pampa region. Even the Yaros maintained some degree of interaction within the doctrinal teachings.

Peace negotiations played a crucial role, especially considering these peoples occupied the vast Vacaria do Mar region, which *missioneiro* chiefs and Jesuit priests considered as areas rightfully belonging to the Missions. This territory was initially formed by the herds released from the 18 *missioneiro* reductions destroyed by the *bandeirantes* in the 1630s (Furlong 1962). In this regard, it is worth noting that the belief in the exclusive spontaneous reproduction of the herds has gradually been losing strength.

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[4] *Bandeirantes* were slavers, explorers, adventurers, and fortune hunters in early Colonial Brazil. They mostly hailed from the São Paulo region.

7.3 Indigenous Shepherds

Recent multidisciplinary research on *Butia* palm corrals in the Rocha Department (Uruguay) and southernmost Rio Grande do Sul (Brazil) indicate that the Guenoa-Minuano and other Pampean peoples mastered bovine and horse herding techniques at the beginning of the seventeenth century. Consequently, the Vacaria do Mar herds were only partially constituted of wild cattle. They entered an area where indigenous people had been managing deer, rhea, and capybara for centuries by naturally trapping them in corrals made of live transplanted *Butia* palms, a species native to the Pampa region (Dabezies et al. 2022; Golin 2022).

Vacaria do Mar encompassed a vast territory that extended from the Uruguay River to the Mirim Lagoon. Within this region, bovine cattle, mules, and horses roamed freely, either bred by the local Pampean people or originating from the early seventeenth-century reductions that indigenous ranchers had to abandon due to invasions by *bandeirantes*. Stray animals from the Prata River region also contributed to the herds. Jesuit documentation mentions various locations within this vast region where *vacarias*[5] were established, including the eastern tributaries of the Uruguay River below the Ibicuí, the Negro River basin, the coasts of São Gabriel (Colonia del Sacramento grasslands), Rosario, Yí, Tacuari, Cebollati, and other rivers and streams in the northern part of *Coxilha Grande*, which is now part of the Oriental Republic of Uruguay, and also rivers in present-day Brazil, such as Jaguarão (bordering), Piratini, and Alto Camaquã, extending to the foothills of the Tapes and Caçapava mountain ranges.

In 1616, the Buenos Aires government already knew of the *vacarias* east of the Prata River, focusing on Maldonado (which extended to where Montevideo is now) and the southern Negro River affluents. Captain Juan de San Martin ordered the withdrawal of 20,000 cattle heads from the region for consumption by the capital (Furlong 1962).

As of 1680, however, tensions escalated into a geopolitical setting as a Portuguese military stronghold was established at Colônia do Sacramento. Consequently, in the late seventeenth century, tribal chiefs in disagreement with Spanish colonialism (and their *missioneiro* allies) now had the option of allegiance with Portuguese representatives, which meant protection or refuge in the Luso-Brazilian citadel of the Prata River and trading opportunities. From then on, *missioneiros* would form a contingency with Spain, while the Pampean groups would join Portugal during all the Iberian wars over the domain of Sacramento and in moments of tension between the kingdoms.

Influenced by this context, in 1701, the Yaro and Bohane expelled the *missioneiros* from the large estate of São José, belonging to the Yapeyú People, located on the eastern bank of the Uruguay River, between the Ibicuí and Quaraí Rivers. Situated in a strategic territory, it was one of the main routes for herds to be driven from the Vacaria do Mar to the reduction cities. After 2 years of warfare and *missioneiro*

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[5] *Vacarias*: extensive grasslands or grazing areas in the Southern Cone of South America. The term originates from the word “*vacas*,” meaning cows, as these regions were historically associated with cattle raising and livestock farming.

retaliation, the Pampeans were relentlessly pursued, defeated, and forced to retreat to the shores of the Yi River (Bracco 2014). Because of the casualties suffered by the men, the Pampean women and children were assimilated into the reduction and forced to embrace a Christian-indigenous way of life. Charrua tribal leaders also organized troops to confront the mission settlers between the Uruguay and Paraná Rivers, notably when the priests granted them land usage rights. This led to intense conflicts during the second decade of the 1700s (Declaraciones 1714). It was during this period that the Jesuit-indigenous settlements grew in strength, hardened their defence systems and their punitive expeditions against the "infidels" (Latini and Lucaioli 2014), wrongdoers, and thieving *gaudérios*[6] who plundered their cattle, all while complying with the demands of the Spanish government.

In the late 1600s, as the *missioneiro* estates were established south of the Ibicuí River, Father José Pablo de Castañeda led an expedition to assess the Vacaria do Mar grasslands and herds. In 1716, he compiled a dossier for the governor of Buenos Aires on behalf of the Society of Jesus, aiming to assert their ownership of the herds. The basis for their claim was that these herds resulted from free-roaming cattle that originated from reductions abandoned during the raids by the *bandeirantes* in the 1630s. *Missioneiros*, vicars, and tribal chiefs provided testimonies stating that "the Tapes and Guarani Indians" were peacefully and undisputedly coming and gathering cows from the Vacarias do Mar. After approximately 40 years of the cattle being taken, they had acquired "tacit consent from the Tapes people, whose ancestors were the original owners of the first cows that founded said herds," as Jesuit Joaquim de Zubeldia stated in 1690. Father Policarpo Duffo had also presented evidence that since 1677, the "Tapes and Guarani Indians were peacefully and lawfully in possession…" (Techo 1897).

The reductions' claim of exclusive ownership over Vacaria do Mar's herds and lands, vehemently advocated by the Society of Jesus, was shaken by the precedent of 1616 given to Captain Juan de San Martin to supply Buenos Aires, and by new Spanish interests in the early decades of the eighteenth century. Having already decimated the herds from the Pampa south of Buenos Aires, which had played a crucial role in the trade between the capital and Santa Fé, the Spaniards shifted their attention to Vacaria do Mar. The ensuing conflicts led them to seek legal avenues for exploiting those herds. The resistance from the missions persisted until all the involved parties, including representatives from Buenos Aires, the city of Santisima Trinidad de Santa Fe, and the Paraná and Uruguay Missions, convened and signed the *Testimony of the Concórdia Agreement*[7] (Pastells 1945).

They reached certain agreements to prevent the depletion of the cattle. That entailed conducting public auctions for a limited amount of 50,000 heads per year

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[6] Historically, the Jesuits identified the men from São Paulo (*Paulista*) who would steal from the Missions using the term "*gáudio*," meaning "vagabond"; those who lived in "*vadiagem*," stealing, robbing, and trespassing on other people's properties. Father Henis, in his diary of the Guaranitic War (1754–1756), refers to these vagabonds, field thieves, and bandits predominantly from São Paulo as "*gaudérios*" (Henis 1770).

[7] Testimony of the Concordia Agreement celebrated between Buenos Aires, the city of Santíssima Trinidad de Santa Fé, and the Missions of Paraná and Uruguay. Buenos Aires, March 3, 1721 (Pastells 1945).

in both cities and prohibiting exploitation during the calving season. The three parties involved in the Testimony were in charge of maintaining checkpoints along the Uruguay River. It was estimated that out of the annual haul of 50,000 heads, 18,000 would be allocated to supply the two cities, 12,000 for Buenos Aires and 6000 for Santa Fe. The remaining 32,000 would be sold according to the interests of the buyers. From a colonial perspective, the Pampeans were not considered the rightful owners of their cattle. Their herds, diligently grazed and cared for, were seized by the bidders who paid the utilization fees to the municipal governments and, of course, the State.

To establish dominance over the grasslands, exploit the cattle ranches, and establish oneself as a rancher, the government needed to implement policies to subjugate the Pampeans. In the 1730s, efforts to convert the western Pampa peoples intensified between the Uruguay River and the Mirim Lagoon basin, driven by the Jesuits' interests and Spanish pressure. This process was documented in the *Mapa de las Missiones de la Compañia de Jesvs*, created by Jesuit Father Joseph Quiroga in 1749[8] (Quiroga 1749) (Fig. 7.1). The map reveals a Minuano reduction in the area encompassed by the headwaters of the Negro, Jaguarão, Vacacaí, and Quaraí Rivers. The region between the left bank of the Alto Negro River and the Cebollati and Jaguarão Rivers is also associated with the Minuano people. Father Quiroga provided an ethnographic description of the Pampean people as well. Regarding the Bohanes, Ganoas [Guenoas], Minuanes [Minuanos]: "They are infidel nations that inhabit the Campanha Grasslands east of the Uruguay River. They share the same customs and weapons […] as the Charruas."

And in the entry about the Charruas:

(i) They are faithless Indians, horse-riding and contentious people, who roam the land south of Laguna Yberá, between the Paraná and Uruguay Rivers. They sustain themselves through hunting and theft. They dress in deer and tiger [jaguar] skins. Their weapons in war and hunting are bows, spears, and a sling with two or three stone balls.[9] It is unknown if they are familiar with the true God, but it is certain that they invoke the Devil in their rituals and sometimes claim to see him.

7.4 Treaty of Madrid: Pampean Tensions and *Missioneiro* Destabilization

In 1737, the Portuguese established the stronghold of Rio Grande de São Pedro on the shores of the Patos Lagoon channel near the Atlantic Ocean as part of their geopolitical strategy. They stationed troops at the southern border near the Chuí Stream

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[8] *Mapa de las Missiones de la Compañia de Jesvs* (Quiroga 1749).

[9] *Boleadeira* (*bolas*): a type of throwing weapon made of stones on the ends of interconnected leather cords, used to capture animals by entangling their legs.

Fig. 7.1 Map of the missions of the Society of Jesus on the Paraná and Uruguay rivers, based on current latitude and longitude observations conducted in the Villages of said Missions; and on the ancient and current reports from the missionary fathers of both rivers. (By Father José Quiroga of the same Society of Jesus in the Province of Paraguay. Year 1749. Copied by Fernando Franceschelli. Rome, 1763. Joseph Quiroga. 1749. Rio de Janeiro: National Library Foundation)

and São Miguel Fort, where the Mirim Lagoon, São Gonçalo channel, and Patos Lagoon formed a western water divide. This frontier became a site of intense violence, with clashes between the *missioneiros* and certain Pampean groups. Still, collaboration with Yaro, Bohane, Guenoa-Minuano, and Charrua tribal leaders also took place. Since this chapter only briefly touches upon the geopolitical movements of the Iberian and National States, we recommend reading the book *Minuanos* (Mazz and Bracco 2010) for a more comprehensive understanding of the Pampeans across the Tape and Eastern Bank[10] territories, along with the references cited in and the classic works on the subject.

Until 1750, the territory of Rio Grande had limited development despite the Portuguese presence along the coastal areas from the Chuí Stream to the north. While state enterprises, such as cattle ranching on the coast, fee collection records, and trade in cassava flour, salt, leather, and beef jerky, were established, the region faced significant challenges, as the *missioneiro* lands served as a trading hub for stolen goods. These included valuable resources such as cattle, fabrics, and even girls. As a result, the Spanish authorities referred to the Portuguese village as a "den of thieves." This context also contributed to the emergence of a social type initially referred to as *gaudério* and later as *gaúcho*.[11] For the indigenous people of the Missions, these terms denoted "grassland thieves," the looters and kidnappers of women and children. They occupied an accessory stronghold that provided a haven to store their stolen goods after perpetrating barbaric acts, including murder, rape, banditry, arson, and various forms of cruelty against their indigenous victims.

After gaining control of the coast, the Portuguese used the Treaty of Madrid as an opportunity to expand their conquests of grasslands to the south and west. News from Europe regarding establishing boundaries between the kingdoms on the turbulent South American border reached Brazil, fuelling ambitions for cattle and offering the possibility of venturing away from the shore into the backcountry, Pampa, and Mission regions. The Pampean areas, particularly the *missioneiro* ones, were home to vast herds with millions of animals raised on their huge *vacarias* and estates. The Portuguese were also enticed by the yerba mate plantations in these areas,[12] as it was an appealing product in European and American markets. The conquerors were interested in a deal struck between the kings of Portugal and Spain, whereby the Portuguese stronghold of Colonia de Sacramento would be exchanged for seven out of the 30 Peoples of the Jesuit-Indigenous Province of Paraguay, specifically those located east of the Uruguay River (Misiones Orientales). The agreed-upon dividing line ran directly through the Southern Grasslands. Without waiting for the official land demarcations, settlers, adventurers, and especially the

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[10] Eastern Bank (*Banda Oriental*) refers to the historical region encompassing the Uruguay River's eastern bank. It was part of the Spanish Viceroyalty of Peru until 1776, when it became part of the newly established Viceroyalty of the Río de la Plata during the colonial period. It corresponds to the territory of modern-day Uruguay and part of the state of Rio Grande do Sul in Brazil.

[11] The term "*gaúcho*" gradually replaces the term "*gaudério*" during the second half of the eighteenth century. It became more commonly used in the written accounts of the conquest of the grasslands as private property. The land surveyors introduced this term to describe the terrain as a "downward slope," indicating that it was below the level and uneven. Essentially, the official society considered themselves to have a higher level of civilization, while those who were marginalized, thieves, and plunderers of the fields, were seen as "off-level," crooked, not upright – "*gaúchos*."

[12] The native *yerba mate* plantations were mainly found in the Rio Grande Shield, in the highlands of the Ibicuí basin, and in the regions of Alto Uruguai and Alto Jacuí.

gaudérios launched attacks on the herds, invading fields, plundering villages, and targeting estates' headquarters, leading to constant clashes with the *missioneiro* militias. From the Pampean perspective, their territory had been divided between the two kingdoms. Along with the Treaty, the Lisbon Court intensified the transfer of Europeans, particularly Azorean couples, to populate the reductions and the south of Brazil. Each nuclear family would receive a grassland area of around 272 hectares.

The land surveyors began the demarcations in 1752, but the following year, rebel tribal leaders and members of the *missioneiro* council revolted, denying access to their Missions. That led to a war that started with significant battles in 1754, later known as the Guaraní War. In 1755 and 1756, the combined Iberian armies gathered at the headwaters of the Negro River. They gradually waged war across the Southern Grasslands, along the Missions Trail (*Caminho das Missões*) (Golin 2015), between the branches of the Ibicuí and Camaquã/Vacacaí Rivers until they achieved a complete victory over the rebellious indigenous forces. Having the Missions territory under control, the Portuguese established settlements in the Povo de Santo Ângelo. In 1757, following the departure of over 3000 *missioneiros*, several villages were founded, giving rise to cities on the left bank of the Jacuí River and along the coasts of the Guaíba and Patos lagoons.

Shortly after, the Rio Pardo stronghold, formed during the Guaraní War, emerged as a significant Portuguese settlement and gained recognition from the *missioneiro* cabildos or city councils (Golin 2014). With its fortress, military garrisons, and officials responsible for collecting fees, it quickly became a focal point of Portuguese occupation. The strategic location, particularly its proximity to the lower Jacuí waterway, made it an ideal hub for goods such as yerba mate, leather, tallow, grease, and troops in the ensuing decades. Recognizing the potential of the vast grasslands and enticed by tales of easy profits and wealth at the border, the Portuguese began relocating numerous Azorean couples to the shores of the Jacuí River, as they could not access the Missions territory at the time. However, the Azoreans and their descendants soon realized that the allocated land was insufficient to sustain their aspirations. They envisioned establishing a stable population, agricultural production, and other industries, prompting many to pursue large land grants and cattle ranches. Unfortunately, this pursuit exacerbated the violence inflicted upon the indigenous peoples, as they now faced further aggression from the military forces and the Azorean settlers on top of the brutality imposed by the *gaúchos*.

7.5 The Treaty of Santo Ildefonso and the Exploitation of Indigenous Lands

In 1777, Portugal and Spain embarked on a new endeavour to pacify their border regions, setting off a widespread encroachment upon indigenous territories. Almost immediately, civilians and the military, with the backing of the State, launched spontaneous invasions as pillaging raids. Eventually, they seized estates, ranches, chapels, villages, towns, and yerba mate plantations extending to the main channels of the Ibicuí and Baixo Jacuí rivers and certain southern tributaries of the Pelotas River. They forcefully occupied these areas before proper identification and demarcation could occur and before any established criteria for the formal occupation could be set forth by Portugal. Luso-Brazilians primarily joined the movement, driven by the historical precedent of the "grassland's land grant letters" (*sesmarias*), wherein each encroacher who expanded the borders stood to benefit from a property allocation of approximately 13,000 hectares.

During the Portuguese expansion into the Ibicuí, Piratini, and Ijuí sub-basins, which began in 1784, the military escorts and troop movements from both empires somewhat deterred raiders. However, before the conclusion of demarcation efforts, the Spanish military and *missioneiro* militias from the Jacuí, Guaíba, Patos, and Mirim lagoons withdrew to the Ibicuí River and its tributaries, leaving the territory vulnerable to the settlers, who enjoyed the protection of the Rio Grande authorities. Armed with unprecedented field surveys, comprehensive cartographic data, correspondence, and detailed diaries, these settlers led commissions faced insurmountable territorial rights disputes between the two kingdoms. The impasses were "resolved" by the War of the Oranges, fought between Portugal and Spain in Europe. This conflict resulted in the Portuguese-Brazilian invasion and occupation of the Missions territory in 1801, extending its frontiers to the Uruguay River, with the southern dividing line at Ibicuí later extended to Quaraí River around 1810. From 1801 to 1828, the lands of the Pueblos de Índios das Missões, initially under Portuguese rule until 1822 and subsequently under Brazilian control, were unjustly appropriated. The seven cities in the Misiones Orientales still maintained some degree of indigenous organization, preserving their cattle ranches, crops, and yerba mate plantations, but they faced constant harassment from intruders and conquering military forces. The indigenous lands and their livestock and improvements became prizes for expansion, transforming officers and soldiers into landowners.

In 1828, the final remnants of indigenous *missioneiro* influence in the Misiones Orientales ended. This occurred during the Cisplatin War when it was no longer possible to maintain any connection with the collaborative experience established during the long Jesuit and chieftaincy period. After a terrible spoliation and loss of territories, the last *missioneiro* tribal leaders were deceived by Fructuoso Rivera's promise in the Cisplatine War and relocated to the north-northwest of the Oriental Republic of Uruguay. This ended an indigenous civilizing experience, with extended families reverting solely to their traditional communal lifestyles. Thousands of them formed the population base of Rio Grande and the provinces of the Prata River.

7.6 The Grassland Raiders: Gauchos

At the forefront of the conflict, the Gauchos and the Spaniards continued their relentless raids, pillaging fields, desecrating chapels, and ravaging *missioneiro* estates. Their actions were facilitated by the withdrawal or negligence of Spanish troops, who abandoned their posts before the demarcation period and the final treaty, maintaining only a small presence in Fort Santa Tecla and sporadic patrols in the Campanha region. The *missioneiros* found themselves particularly vulnerable to the barbarism that swept across the territory south of the lower Jacuí River and in the southern Ibicuí basin. The land surveyors diligently recorded their experiences as they ventured along the Negro, Camaquã, Vacacaí, and Ibicuí rivers.

The marauding crowds, driven by greed and violence, forcefully annexed a region spanning 300 by 500 kilometres, encompassing the Sierra foothills, the Rio Negro headwaters, and the Mirim Lagoon. The *gaudérios* and *gaúchos*,[13] regarded as notorious raiders and smugglers, were held responsible for the difficulties faced by colonial settlements, border conflicts, and even wars between nations. They alternated between fostering alliances in times of peace and resorting to barbarism during the war.

Consequently, the second clause of the Preliminary Treaty of 1777 (Tratado 1777) stipulated that the leaders of any invasion, regardless of their nature, would be subject to the death penalty. The nineteenth clause forbade any unauthorized land occupation without the mutual consent of authorities from both Kingdoms. Along all neutral borders, it was imperative to prevent the harbouring of thieves or murderers, with governors coordinating efforts to apprehend and eliminate such individuals, imposing the harshest punishments. Moreover, fugitive slaves, considered valuable national assets, would be returned to their respective authorities.

Ongoing conflicts with the *gauchos*, smugglers, and other intruders accompanied the land demarcations, inflicting severe harm on the *missioneiros*. These raids denied them the opportunity to negotiate their livelihoods and livestock or even decide whether to stay within the territory, now under a new sovereign amidst shifting frontiers. Consequently, the surviving families were forced to adopt a traditional community model, departing from the *missioneiro* system. A handful of tribal leaders managed to retain portions of land for grazing and agriculture despite the initial onslaught by the Luso-Brazilians, who were interested in the looting and subsequent privatization of indigenous lands, which were relinquished by those who possessed Portuguese land grant letters. Meanwhile, the Pampeans roamed the neutral grasslands and the southern tributaries of the Ibicuí River, continuously moving their *toldarias* and herds across Iberian borders.

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[13] *Gaudério* and *Gaúcho* are two terms that refer to the same social group, which gradually took shape over time. The term "*gaudério*" was initially used by priests and missionaries to classify thieves and bandits who would attack and plunder the reductions and their estates. It was commonly applied to individuals such as the *Paulistas*, *mamelucos*, and *Bandeirantes*, stemming from the word "*gáudio*." Please refer to the specific note for more details. Eventually, the term extended its usage to encompass the entire region influenced by the Missions. On the other hand, the term "*gaúcho*" emerged due to identifying this social group within the context of colonial property. It gained prominence in the second half of the eighteenth century and was always closely associated with the term "*gaudério*." Please refer to the specific note for additional information. As time passed, "*gaúcho*" underwent a symbolic reinvention, coming to represent a regional identity or regional archetype. At the same time, "*gaudério*" became associated with a way of life characterized by wandering and nomadism.

7.7 The Pampeans in Cartography

The spatial distribution of Pampeans depicted in Quiroga's maps (Fig. 7.1) is of great interest, as they stayed in their traditional regions despite the chaotic events unleashed by the Treaties of Madrid (1750, Fig. 7.2) and Saint Ildefonso (1777), as well as the turmoil caused by the 1801 war. Quiroga's cartographic records indicate that the Bohanes inhabited the area between the headwaters of the Quaraí (north), Daymal (south), Santa Maria (east), and Uruguay (west) rivers. The Ganoas [Guenoas], currently considered part of the Minuanos or related ethnic groups, resided between the junctions of the Santa Maria, Queguay, and Vacacaí rivers. As astutely noted by Quiroga, the Charruas were still located between the Paraná and Uruguay rivers, as they had not yet significantly encroached upon the territory of the Bohanes/Yaros on the eastern side of the Uruguay River.

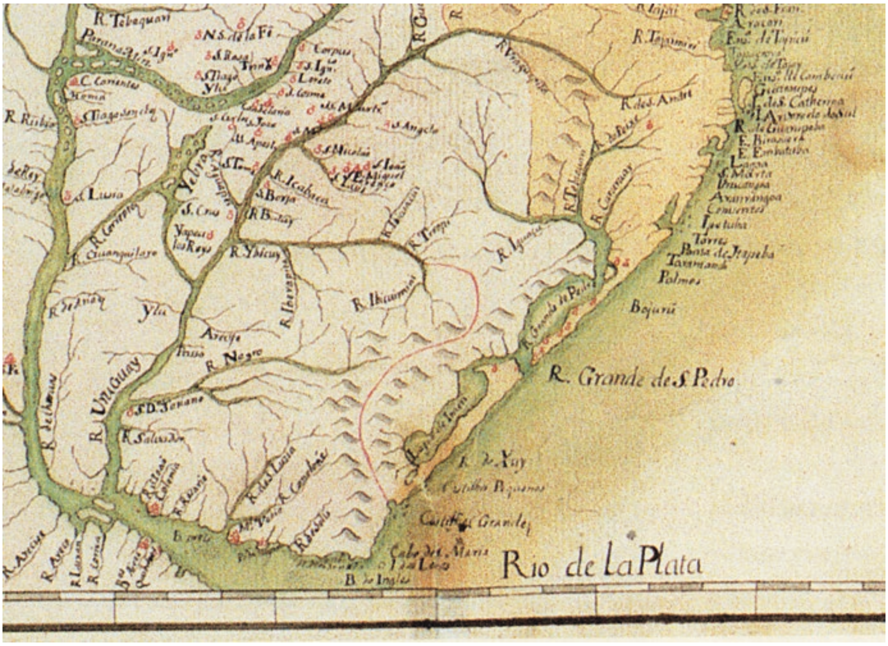

Fig. 7.2 Border detail in the *Mapa das Cortes*, 1749, illustrating the Treaty of Madrid, 1750 (red line). The depicted boundaries cut through the Southern Grasslands region. Starting from Castillos Grande, the line passed between the headwaters of rivers and streams in Coxilha Grande, continued through the headwaters of the Negro River, and followed to the Ibicuí River's primary headwater*. It then traced the entire Ibicuí River's course until it reached its mouth at the Uruguay River. From there, it followed the waters to the Peperi Guaçu. (Source: Brasília: Army Documentation Center. Rio de Janeiro: Itamaraty Map Library. Porto, Portugal: Municipal Public Library. *Note: The location of the Ibicuí River's headwater was a point of contention among land surveyors and a cause for the treaty's revocation in 1761. The Portuguese argued for the headwater in the present-day Santa Maria River, which they referred to as Ibicuí Antigo, while the Spanish claimed it to be in the Ibicuí Mirim, a position that is currently accepted)

According to Father-Superior Bernardo Nusdorffer, the Christianised Minuanos were crucial in organizing the vast Santa Tecla *missioneiro* estate, where non-*missioneiro* relatives would visit and coexist. These visits often brought important news for the reductions, particularly regarding the Portuguese and their dangers, as was when Quiroga completed his map. In 1752, Father José Cardiel created another map, *Mapa de la governacion del Paraguay*, intending to challenge the frontiers established by the Treaty of Madrid. In this map, the region situated between the Ibicuí and Negro rivers is generically referred to as "Estates" or "Guarani Estates," indicating their association with the reductions without detailing the specific territories occupied by different indigenous groups (Fig. 7.3). Since the Jesuits did not differentiate past *missioneiros* and non-converted indigenous peoples, the Pampeans were not depicted on the map. Consequently, the "infidels" appear in the highlands of the left bank of the Negro River, precisely in the area identified in other maps and documents as belonging to the Minuanos.

When the Spanish authorities responsible for the land demarcations outlined in the Treaty of Madrid arrived in the region in 1752, as indicated on the *Mapa de las*

Fig. 7.3 Frontiers of friction and conflicts. The indigenous core of the missionary estates and Pampean peoples ("infidels") were pressured by the "Spanish estates" encroachment from the south and the intrusion of the Portuguese-Brazilians from the East. The lands between the Ibicuí and Negro rivers, generically identified by José Cardiel as estates ("*estancias*") and "Guarani estates," belonged to the reductions and were managed by tribal chiefs. In the *missioneiro* estates there were Pampean *toldarias*, such as the Guenoa-Minuanos, immersed in the San Miguel People's one. Detail. 1752. *Mapa de la Governacion del Paraguay y de la de Buenos Ayres con la linea divisoria de las tierras de España y Portugal ajustada entre las dos Coronas año 1750 cuya posesion se pretende tomar este año de1752, Ponense tambien las tierras que tocan a Portugal segun la linea del papa Alejandro VI que antiguamente se ajustaron las dos coronas.* (José Cardiel (S.I.). Simancas General Archive)

Missiones, Chief Moreira's group seized their horses in Castillos Grande. Pursued by the Iberian troops, their *toldaria* was discovered 40 leagues away, leading to a battle where the horses were eventually recovered (Golin 2004). Gomes Freire, taking advantage of the situation, managed to attract the Pampeans by saving them from the death sentence imposed by Marquis de Valdelírios, the initial commissioner appointed by Madrid. In 1754, after initially fighting alongside the *missioneiros* during the Guaranitic War with 200 horsemen, Moreira switched sides when General Gomes Freire de Andrada proposed an agreement at the Passo do Jacuí encampment. As part of the agreement, Moreira's lands south of the Mirim Lagoon would be officially recognized in exchange for abandoning the rebel cause.

Father-Superior Nusdorffer also documented the deep-seated hatred of the Pampeans towards the Spaniards. Within the same reduction, all the major ethnic groups assembled under the jurisdiction of Yapeyú. They were present in the city and established their *toldarias* and herds in the region between the Ibicuí and Quaraí rivers, which served as their primary estate. According to the Jesuit authorities, "their estate accommodated all the Charrua infidels, Mohanes [Bohanes], Yaros, Guenoas, and Minuanos, seeking refuge due to their strained relations with the Spaniards and their inability to sustain their livelihood elsewhere apart from the Yapeyuan Indians, their kin" (Cortesão 1969). Due to various contingencies, this territory became the final refuge for the remaining Charruas and Minuanos.

Father Quiroga's ethnographic endeavours were magnified by the topographical assessments carried out by the land surveyors between 1752 and 1761. Cities, towns, estates, yerba mate plantations, and villages were meticulously mapped, often utilizing on-site measurements, showcasing the extensive network of *missioneiro* estates. Notable among the depicted events was the significant loss of the Povo de São Luis estates and grasslands north of the lower Jacuí River, resulting from the treaty signed by *missioneiro* cabildo and General Andrada in 1754, which designated the area as a frontier. The Missions also relinquished a portion of *Vacaria Nova* encompassing the lowland region between the Taquari and Pardo rivers and their herds. Concurrently, in 1757, the land surveyors concluded the mapping of the *missioneiro* estates, particularly those situated south of the main Ibicuí – Ibicuí Mirim riverbed, including the initial settlements that mirrored the seven cities slated for transfer under Portuguese jurisdiction, pending confirmation of the demarcation enactment. This level of detail was achieved through access to Jesuit cartography, most notably that of Father Tadeo Henis (Barcelos 2006) and indigenous *missioneiro* sketches.

Despite the termination of the 1750 Iberian agreement through the Pardo Treaty (1761), prompted by international circumstances, the uprising of rebel tribal leaders, and significant discrepancies in land demarcation, the remarkable cartographic endeavours, diaries, memoirs, dispatches, and letters produced by expedition members, Jesuit priests, and indigenous *missioneiros* would not be lost. During that period, others were also committed to describing the spatial organization of the region, such as the Portuguese land surveyor Miguel Ciera. Having served in the border commissions from 1752 to 1761, he compiled the comprehensive frontier map, *Tabula Nova*, finalized in 1782. He proved instrumental in the activities of the

Treaty of Saint Ildefonso commissions, initiated 2 years later. Ciera reaffirmed that the "Minuanes" predominantly occupied the region between the Upper Negro River and the Cebollati basin, lands that had always been their own. He further indicated that, due to the 1750 dividing line, most of that nation would remain within Luso-Brazilian territory (Ciera 1782). Once again, they would be dispersed across the border territory, including the neutral area.

In 1761, after the Treaty of Madrid revocation and the resumption of antagonisms between Portugal and Spain during the Seven Years' War, Antoine-Joseph Pernety settled a symbolic representation of the Minuano people. During this period, Governor Pedro de Cevallos took control of Colônia do Sacramento and was in Montevideo leading an expedition to occupy the Santa Teresa and São Miguel fortresses, the village of Rio Grande, and its surrounding lands and waters. During this time, the French painter, while passing through the Plata River, created the *Plan de la ville de Montevideo* (Plan 1763). This painting showcases the geographical space, the city, and the harbour with its ships. Notably, it includes the portrayal of an indigenous Minuano figure adorned with a striking cape (*cayapi*) featuring ethnic motifs (Fig. 7.4), serving as an expression of their cultural identity.

The process set in motion by the Treaty of Saint Ildefonso heightened existing tensions. It began with Cevallos' offensive and his occupation of the Rio Grande coast in 1763. Subsequently, in 1764, the Portuguese defence launched a dynamic

Fig. 7.4 The Minuano as a representation of human identity in *Plan de la ville de Montevideo*. 1763. Antoine-Joseph Pernety, 1716–1796. *Histoire d'un voyage aux Isles Malouines, fait en 1763 e 1764: avec des obseruations sur le detroit de Magellan et sur les Patagons*/par Dom Pernety; tomo premier. (Fondo Antiguo de la Biblioteca de la Universidad de Sevilla. Digitalization: Rio de Janeiro: Itamaraty Map Library)

war effort, resulting in incursions into the lands west of the Guaíba River, encompassing the Patos Lagoon region and the southern reaches of the Lower Jacuí. The invaders seized *missioneiro* chapels and estates along the lower Jacuí's southern bank's tributaries, appropriating livestock and agricultural resources, including yerba mate plantations. Despite an ambitious expedition led by Governor Vertiz y Salcedo of Buenos Aires in 1773, the attempt to expel the intruders and the *missioneiro* troops failed. However, the following year, Marquis de Pombal contemplated ousting the Spaniards from Rio Grande, leading to the declaration of war in 1774 and its successful conclusion by 1776. Throughout this period, the Portuguese-Brazilian authorities already granted grassland land grant letters for the region, focusing primarily on the present-day city of Cachoeira do Sul. During this time, the area was both Spanish and indigenous territory.

However, the War of Reconquest, which achieved significant victories in the territory of Rio Grande, had far-reaching consequences. In response, the Spanish forces captured Santa Catarina and Colônia de Sacramento and were poised to march back into the territories they had recently lost. At this pivotal moment, Portugal proposed a peace treaty, ultimately signed in Saint Ildefonso, Spain, on October 1, 1777.

Under the mounting pressure of land privatization encroaching from the coastal areas, the Pampean people, particularly the Minuanos, persisted along a stretch of land extending from the Mirim Lagoon basin to Santa Maria da Boca do Monte, encompassing the waters that flow towards the Atlantic coast of Rio Grande do Sul and the Prata River. In a letter penned in 1786, Lieutenant José Carvalho da Silva informed Colonel Rafael Pinto Bandeira of his encounter with Minuano *toldarias* at Rincão Santa Maria (currently District of Boca do Monte, within the municipality of Santa Maria). These *toldarias* had been established in 1784 and were led by five tribal leaders, comprising a population of 300 men, 270 women, and over 420 children. Additionally, they oversaw many domesticated animals and their herds of cattle.[14]

During the 1787 land surveying efforts to establish boundaries between Santa Tecla/Bagé and Santa Maria, the commissioners encountered Minuano *toldarias* in the Cacequi river basin. The principal tribal leader, Miguel Caraí, had relocated his *toldaria* from the Mirim Lagoon area to join other leaders in the newly expanding frontier, settling near the springs of the Inhatium marsh. Tribal chief Tajuy headed the group at the bend of the Cacequi [Cassequey] river, just before its confluence with the upstream Ibicuí. It was customary for tribal leaders to visit the land surveyors' camps, as recorded by José de Saldanha on March 14, 1787: "We set up camp on the east bank of the Arroyo de Nachiu [Inhatium], where our carts and reserve horses were already waiting for us. […] It was in this camp that the Minuano Indians first visited us."

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[14] The Portuguese colonial government granted the Rincão de Santa Maria through a land grant letter (*carta de sesmaria*) to Francisco Antônio Henriques de Amorim in 1789. Later on, he sold the estate to Father Ambrósio José de Freitas (Beltrão 1979).

The Topographic Plan (*Plano Topográfico*), considered the comprehensive map of the demarcation efforts, was endorsed by the main commissioners José Varela Ulloa (Spain) and Sebastião da Veiga (Portugal). It meticulously depicted the "Passo dos Minuanos," a significant crossing point on the Jaguarão Chico River. This location served as a vital link to the "Povoação dos Minuanos," as indicated on José Saldanha's 1801 map, which already portrayed the Portuguese-Brazilian conquest of the Missions and the expansion of the frontier encompassing the Jaguarão, Santa Maria, Ibicuí, and Uruguay rivers. As the invaders claimed domain over the Pampa territory, the Pampeans embarked on a strategic relocation, transferring their *toldarias* and livestock to the Ibirapuitã sub-basin situated within the neutral territory, as delineated by the *Status quo of 1804* agreement enforced by the Portuguese-Brazilian and Spanish troops, which remained in effect, albeit with numerous encroachments, until 1810 (Golin 2002).

The chorographic map of the Captaincy of São Pedro[15] created in 1801, provides one of the earliest recorded accounts of the Pampean concentration of surviving Charruas and Minuanos in the Upper Ibirapuitã region within the southern basin of the Ibicuí River (Fig. 7.5). It was created by Colonel Francisco das Chagas Santos, who later took charge of the Portuguese government of the Missions. The map labels the area as the "Mountain range inhabited by the infidel Charrua and Minuano Indians." Initially part of the land demarcation commission, Santos would become an avid usurper of the *missioneiro* cabildos, Charrua, and Minuano lands.[16]

7.8 Saldanha's Records About Minuano and *Missioneiro* Indigenous People

In a document dated January 28, 1787 (*Diário Rezumido e Historico*), José de Saldanha, an astronomer and land surveyor commissioned by Portugal, vividly depicted the hardships endured by the *missioneiros*.

(i) Ascending and descending different points of hills, which are divided by the Taquarembó, and end in the meadow on the eastern bank of the Ybicuy River, […] we crossed the Santa Anna stream and camped on the southern bank of the Taquarembó […].
(ii) Observed latitude: 30°49′8″ [S].

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[15] Chorographic map encompassing the Captaincy of São Pedro, part of the government of Montevideo, including the city of the same name, and the important individual geographical surveys that will be conducted in the First Division of the Demarcation of Limits of South America, by the respective engineers and astronomers in all the territories that should be examined for the knowledge of the Portuguese and Spanish Courts, as ordered in the Preliminary Treaty of Limits of October 1, 1777. / Constructed and drawn by Colonel Engineer Franco das Chagas Stos. Lisbon: Military Archive, currently the Army Historical Archive.

[16] Regarding the theft of indigenous lands by Chagas Santos, refer to Saint-Hilaire 1974 and Chaves 1978.

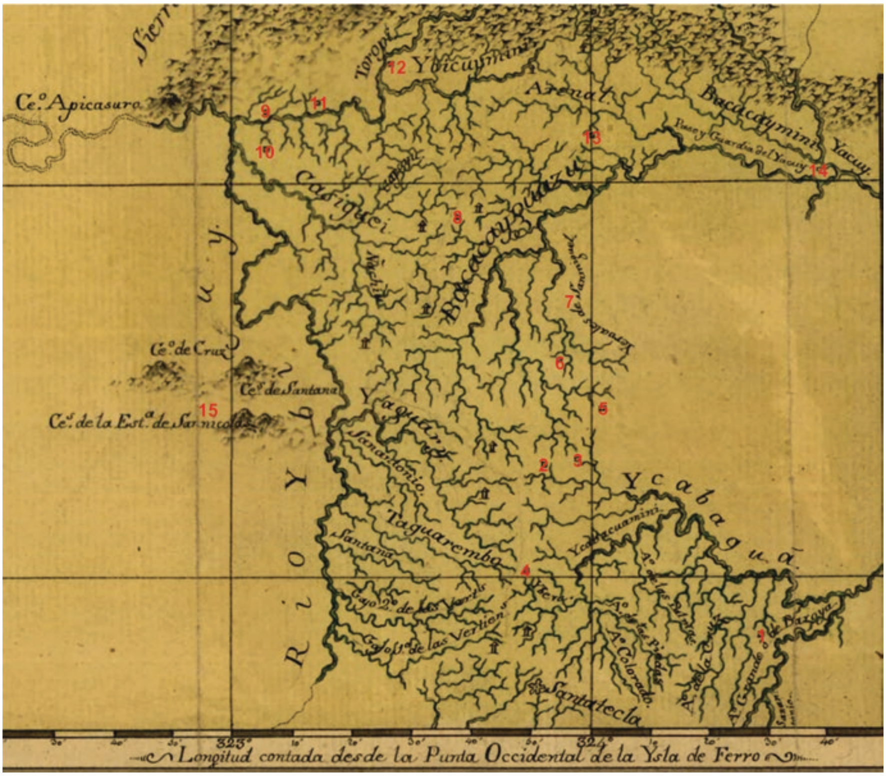

Fig. 7.5 Among the 38 main *missioneiro* estates (along with their villages or *rancherios*) depicted in the 1786 *Chorographic Plan*, 15 were situated in the primary course of the Ibicuí – Ibicuí Mirim rivers and their southern territory. These *toldarias* are marked with numbers based on the conventions of the border commissions. They were the first to be plundered and occupied by the *gauchos*, settlers, ranchers, and Portuguese authorities. Throughout the vast frontier region, up until 1801, the indigenous communities managed to maintain their presence in *toldarias* located to the north of Monte Grande, particularly in the tributaries of the Ibicuí Mirim, the tips of Piratini and Ijuizinho, and on the right bank of the Jacuí River. *Plano corografico de los reconocimientos pertenecientes a la demarcacion del Art. 8°. del Trato. Preliminar de Limites de 11 de octe. de 1777 practicados por las segundas subdivisiones española y portuguesa en orden a desatar los dudas suscitadas entre sus respectivos comisarios.* 1786–1788. (Library of Congress Geography and Map Division Washington, D.C.)

(iii) […] Pleasant and delightful hills, abundant with water sources, form this countryside, mainly on the northern side of the Santa Anna stream, as mentioned above, where there used to be a large estate of the Indigenous Tapes, with the same name, belonging to the Missions People: it was depopulated and driven away by the continuous thefts of the Gauchos, wandering nomads of the grasslands, who moved to the western side of the Ybicuy-guasu River, along with

> the remaining horses and livestock. Now, only wild and untamed (*chimarrão*[17]) animals graze here (Saldanha 1786).

As Saldanha advanced towards the new Ibicuí border of the Southern Grasslands, he could see the atrocities performed by the "*gauchos*" as well as the trails they used to move contraband, supplying merchants, jerky artisans, and landowners from the territory of Rio Grande. The newly formed oligarchy had its origin tainted by theft and the resulting violence. On March 9, 1787, the land survey expedition led by Saldanha arrived for the second time on the banks of the Icabaquá river (now Camaquã), near "the second branch of its headwaters," where "we camped on its northern bank, next to a crossing that had been newly made and opened by the *gauchos*, or drifters of the grasslands."

The *gaucho* intrusion in the Missions and Pampa territory led to a change in the toponymy. In February 1787, Saldanha observed that one of the tributary streams of the Seival (Ceíbal, a Negro River tributary) had been renamed "Arroio das Pedras", "currently titled by the *gauchos*."

The land demarcation expeditions through territories undergoing profound transformations, including the tragic ethnocidal fate of the indigenous peoples, lend great significance to José de Saldanha's Diary. Within its pages, one can find the Minuanos' deep connections to various aspects of their environment, including the naming of natural phenomena, topography, cartography, and ways of life. Saldanha, the astronomer, bolstered the argument for identifying the "Vento Minuano" (Minuano wind) by tracing its origin to Rio Grande, where it was said to come "from the direction of the Minuano Indians." The same wind is known as "Pampeiro" in the Eastern Bank because it blows from the Pampas of Buenos Aires in that direction. Common names transformed into enduring records, such as the "Passo de Jozé Minuano" on the Ycabaquá River and the "Povoação dos Minuanos" on the southern bank of the Jaguarão River.

As we delve into Saldanha's writings, it becomes evident that he was keen on documenting significant human experiences, even though with biases that were a product of his time. As described in his accounts, the Pampean people are depicted within the context that marked the end of the eighteenth century.

(i) The Minuanos do not have as pronounced noses and cheekbones as most indigenous people. They are mainly robust and well-built, but the women are generally of average height and their features closely resemble those of the Americans. Their hair, which does not grow long, falls loose and curly, covered down their backs down to their heels by *cayapis* – large mantles made of scraped and tanned leather, with fur inside and flesh on the outside. These mantles are fastened with a strip of the same leather over the shoulders and around the neck.

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[17] *Chimarrão* (adjective): wild, startled, and untamed cattle. It is also the "name given to the wild dog that inhabited large desert areas of the Pampas until the mid-nineteenth century, posing a threat to the resident populations," as well as "a constant menace to domestic animal husbandry (these dogs, which attacked the cattle, were pursued and exterminated by the hundreds; today, they constitute a Uruguayan canine breed recognized by dog fanciers)" (Schlee 2019).

They are wrapped around the waist, reaching the knee, with a cotton cloth wrapped in a spiral.[18] These are their typical garments.

(ii) The *cayapis*, which they make from deer or calf skins, scraped, tanned, and sewn together, are adorned on the outer side, the flesh side, with stripes of red and grey running lengthwise. They get this colour from the iron ochre dirt found abundantly in the streams of the branches of the Cassiquey River[19] [Cacequi].

In the field, he witnessed the Minuano way of living:

(i) Their itinerant homes are usually installed on some open hill [*coxilha*] and rarely near the woods. They comprise small mats made of a board-like straw and a few cattle hides that poorly cover three sides of the house, including the upper part that serves as the roof. They prefer to use woven mats to let rainwater run off. The fourth wall serves as the doorway. Their rugs [*alcatifas*] or floorings are bare earth and sometimes small hides. Inside, they can accommodate only five persons. They sleep there, eat there, and cook there, but they keep them cleaner than their own bodies. These dwellings are called "*toldos*"; and when gathered, they become a "*toldaria*."

Historically, the Minuanos were "divided into various bands or tribes," which formed "their chieftainships." These leadership positions could be based on "descent or mutual agreement." Saldanha described some chieftains, including Salteinho, Maulein, Batu, Tajuy, and "D. Miguel." The latter had "spent over twenty years in a Portuguese Estate working as a cowhand, from which he escaped to return to his people." Miguel Caraí was described as "shorter" than the others, "plump, with a cheerful countenance, and more reasonable." He carried "a yellow-trimmed Chifarote [short, straight sword]," possibly obtained from some ally on the Rio Pardo border. The Pampeans would often visit this Portuguese stronghold at the confluence of the river bearing the same name and the lower Jacuí, both as a sign of peace and for trade purposes.

(i) Among the Minuanos, others tie their hair and heads with a small dirty scarf. Some, especially those of Chief Tajuy, wear the *sisi*, a small flat figure made of yellow brass, about an inch long, inserted through a soft opening they make in the lower lip; others use a sewing needle in the same place. […] This Chief Tajuy covers his head with a round mitre[20] made of jaguar skin adorned with engraved brass discs and red cords hanging from it.

Tajuy was "tall, well-proportioned, and agile." Salteinho, the elder. He bore "a three-line cross marked on his nose and eyebrows, made with a hot iron, which

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[18] This piece of Minuano clothing is currently called a "*chiripá* skirt."

[19] In Saldanha's account, the name "Cassiquey" originates from the presence of several indigenous *toldarias* led by Minuano tribal chiefs along its banks. "The Indians gave it the title of river, creek, or the chief's water – Cassique-y." Diary, record dated April 3, 1787.

[20] Mitre: in this case, a high-crowned hat or cap.

remains greyish; one of his wives, an elderly woman they call Maria Rosa, wears an identical cross." Batu was "tall, old, stern, and unattractive."

The Minuanos sustained themselves on a diet primarily composed of "lightly roasted" beef or venison wherever they travelled. They also consumed crested caracaras and other similar birds of prey or occasional ostriches. Using yerba mate was deeply ingrained among them, always associated with tobacco, much like other indigenous peoples of South America.

> (i) The mate drink, [the minuanos] do not put it down as long as they have this herb, as well as chewing tobacco; and they keep the chew either between the upper lip and the teeth, or they take it out of their mouth and place it behind their ear, where they keep it until they chew it again. Few smoke a pipe or a rollup, and they all greatly enjoy drinking *aguardente* (distilled spirits).

Given the Pampean way of life, weapons were invariably also tools for working or providing sustenance. According to Saldanha, they used weapons such as…

> (i) Arrows, which they carry in a leather quiver, slung over their backs. These arrows are only used in times of combat and rarely employed for hunting. That may be because acquiring iron is difficult for them, and it requires effort to craft arrowheads, so they reserve them as tools for their safety. The arrows are at most 60 centimetres long, and the bows are proportionally sized. Whether on foot or horseback, they are skilled at shooting them. Their spears are long, straight poles that end with 20–40 centimetres of dagger or sword, and before attaching them to the wood, they adorn them with an ostrich feather flower-shaped ornament. They reach about two of their heights. Swift and agile, they wield them on horseback at full gallop. In addition to being used as weapons, these spears are sometimes employed to prod cattle or bulls in the field or even to fend off tigers [jaguars].

Like other pastoral peoples worldwide, the Minuanos used weapons typical of horsemen, like the short bow and the long spear. In addition to these, they also employed the bolas and the lasso.

> (i) The bolas and the lasso, ordinary and necessary tools of the dwellers, who roam these grasslands, originated from them. With these implements, they capture wild mares and colts in the grasslands, as well as gentle horses found among these bustling herds. Through arduous labour, they eventually tame them, keeping them restrained and weakened from the scarcity of sustenance and then using them bareback, with only a tiny piece of leather as a makeshift saddle.

As part of their ensemble, they carried a particular type of knife, the Flemish knife, which became a regional custom. It would always be tucked into a raw leather sheath and placed at the back between the cotton loincloth and the waist. This "way" of carrying the knife can be associated with a suitable "technique" employed by those who rode horses and skilfully handled bolas, lassos, bows, and lances. Similar to the Minuano attire, it is linked to locally sourced materials.

(i) Their attire consists of a shirt worn over a cotton loincloth and sometimes a *bichará* poncho. The ponchos, widely used throughout this continent, have a rectangular shape like a blanket, with an opening in the centre through which they are put over the head, resting on the shoulders and falling halfway in the front and halfway in the back. They come with different qualities and values. The most common ones here are called *bicharás*. They are made of thin wool fabric, imitating Burel[21] with stripes of different colours and a short fringe around them. They exceed the price of one and a half silver pesos. In Buenos Aires, there are more refined and well-made ones, known as *palas*, which sell for six or eight strong pesos. They also produce finer cotton ponchos in various colours, valued at 12–16 pesos at the Missions. These resemble the luxurious ones made of fine cotton fabric with delicate-coloured stripes, manufactured in Paraguay and neighbouring towns, and their cost ranges from 90 to 100 strong pesos. Wealthier individuals also use them as bed covers.

Men would marry "multiple women, ranging from two to five." In preparation for marriage, the older women would educate the unmarried ones. They were told to "serve their husband, gather firewood, cook the roasts for meals, saddle the horses for those suitable (only the tribal chiefs and their wives)." Losses and mourning were expressed through dramatic rituals, similar to other indigenous peoples:

(i) These Minuano Indians express grief when a close relative dies by inflicting wounds or small cuts on their backs. Some mothers mourn the loss of their children very brutally, cutting off the phalanges or the outer parts of their pinkie fingers at the joints.

These hardships were not uncommon for the Minuano people during that period. They had to endure the smallpox epidemic. "The pox has significantly reduced their generation in recent years, taking away all the children."

Whatever the Minuanos could not provide within their habitat, they sourced outside.

(i) When faced with necessity, they embarked on journeys to certain southern settlements in the Missions, or Guarda de São Martinho, or finally to the Portuguese estates and the Rio Pardo border. They would bring some of their horses caught in the fields, pairs of bolas [*boleadeiras*], and new *cayapis* to exchange for yerba mate, cotton cloth, Flemish knives, tobacco, spirits, or a few harnesses.

Saldanha's narrative acts like a testimony, as he witnessed, lived among and conversed with the Minuano people in different settings. While camped near the right bank of the Cassiquey River, he wrote, "On the other side of this stream, along the adjacent hill, there lies a large grove, near which a group of Minuanos had also settled for the day, as they were headed to the cattle and wild horse race."[22] He stayed on the southern coast's main crossing, half a league away from the "Minuano Toldaria

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[21] Place in Portugal with a tradition in sheep wool manufacturing.

[22] Diary, record dated March 18, 1787, at the observed latitude: 30°11′49.15″S.

of Cassique Tajuy," who visited the frontier commission several times.[23] At the Mbatobi stop, "next to a post upheld by the San Miguel community [*missioneiros*], a chief and several Minuano Indians appeared."[24]

José de Saldanha knew he was witnessing the decline of a dwindling people.

(i) When the Spanish did not settle in the southernmost regions of Lagoa Mirim like the shores of the Sabuiaty River [Cebollati], the largest indigenous *toldarias* were established there. However, once the Spanish drove them out, they gradually retreated farther north, towards Cerro de Mbatobi [Batovi]. It is where their remaining *toldarias* are. Sometimes, they even venture as far as the eastern coast of the Uruguay River.

Now, mighty enemies, backed by conquest and settlement projects, occupied their lands. They lived in freedom amidst the Spanish and Portuguese. However, it was estimated that there were only "thirty to fifty individuals, on average, in each *toldaria*, which leads me to believe that they do not exceed two hundred in their current state." He speculated that these Minuanos might be "captured and distributed among the civilized peoples of both nations"[25] [Portuguese and Spanish].

7.9 Portelli and the Usurpation of *Missioneiro* Lands and Possessions

Another surveyor, Captain-Engineer Alexandre Eloi Portelli, also documented in the *Diary of Marches*, completed in 1788, the dismantling of the network of estates, settlements, and *missioneiro* chapels. While passing through the "rincões of the Vacacaí River and the great trail of Santa Catarina," he encountered "a multitude of free-roaming cattle," now without the herding of the indigenous cowhands from the native ethnic groups that comprised the *Pueblos de Indios* (Indian villages). Faced with this situation, he proposed a state policy, relying on the indigenous herds for forming assets and primitive accumulation for the invaders. According to Portelli, as they were in the new "domains of Portugal," as per the frontier treaty, they could serve as the material foundation for future settlers and even be appropriated by private estates and crown estates. He suggested they should be cornered

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[23] Diary, record dated March 20, 1787, at the latitude: 29°53′24″S. *Bagual*: Uncastrated, intact horse, generally considered wild, untamed, or partially tamed; skittish and easily startled.

[24] Diary, record dated March 31, 1787.

[25] Brief and historical diary or Geographical Account of the Marches and Astronomical Observations, with some notes on Natural History, by Paiz. First Division of the Demarcation of South America. 4th Campaign from 1786 to 1787. Under the supervision of Brigadier Sebastião Xavier da Veiga Cabral da Camara, Governor of Rio Grande de São Pedro, and Chief Commissioner. By José de Saldanha. Bachelor of Philosophy, Graduate in Mathematics, Geographer, and Astronomer of His Most Faithful Majesty, in the 1st Part. Rio de Janeiro: National Library Archives, 1929, v.51, p. 233–238, 241, and 281.

(i) along the riverbanks and streams, and then accounted for by the Royal Treasury or distributed among the new settlers of these lands that could make the continent more fertile and abundant with their production, bring themselves happiness, and increase the rights of His Majesty (Portelli 1788).

In other words, the tragedy of the indigenous ethnic groups that comprised the Missions and the territorial strangulation of Pampa's people would result in the "happiness" of the Portuguese-Brazilian vassals. Among them was Captain Portelli himself, who would later participate in the process of plunder through military conquest up to the Uruguay River, carried out 13 years after his frontier commission records, thus becoming a landowner as well. Within this extraordinary usurpation of the land's former owners, the abandoned peach trees of the estates, settlements, and chapels remained as memory. As enduring remnants, these orchards resisted within the shared space of the intruders.

The three sectors that diverged during the land surveys remained indissoluble, with Spain's immersion in various wars until the Portuguese-Brazilians militarily invaded the *missioneiro* territories, the Jê peoples, and the Pampa peoples, and conquered them up to the Uruguay River, starting in 1801. They intensified the occupation, possession, and land registration of communal lands, cattle, yerba mate plantations, and cities belonging to the indigenous peoples. What remained of the *missioneiro* organization was extinguished in 1828 during the exodus led by Rivera in the Cisplatin War.

During the last decades of the eighteenth and early nineteenth centuries, several extended families returned to their traditional way of life, reorganizing villages in their ancestral territories or alongside relatives who remained in more remote locations. Thousands became workers in various manual labour jobs; many lived as artisans, musicians, teachers, sailors, builders, painters, and drovers. Only a few became landowners, while others embraced the *gaucho* way of life. In this devastating phenomenon, the wombs of indigenous women became the fertile ground where the conquerors' lineage took root. Predominantly, it was from the indigenous women that the caboclos and southerners were born.

The barbaric Portuguese-Brazilian attacks also led to the adoption of survival strategies through isolation in mountains and dense forests.

7.10 The Pampean Confined on the Border

At the same time, another colonialist movement from the Prata River targeted the Pampeans as their enemies, blaming them for the difficulties faced by Spanish settlers, mainly through the establishment of estates for raising cattle. In 1802, Portuguese military officer João Francisco Roscio wrote to Paulo José da Silva Gama, the governor of Rio Grande, advising against the Spanish enemies' movements. Lieutenant Colonel Quintana, from the Spanish army, was encamped on the shores of Arroyo San José, between Colonia del Sacramento and Montevideo, leading an army of a thousand men. They claimed their objective was to "exterminate the savage Charrua and Minuano Indians," accusing them of "harassing" the landowners. However, Portuguese-Brazilian officers believed they could execute a tactical manoeuvre transitioning from suppressing the indigenous population to "reconquering the *Sete Povos das Missões*."

Concurrently with the Missions invasion, characterized as "*malón*" for its banditry and looting, a similar event unfolded in the frontier region of the Jaguarão River basin. This area held significant historical importance as the ancestral territory of the Minuano people. Operating from a base in Cerrito, located in the present-day municipality of Jaguarão, RS, this incursion mirrored the tumultuous nature of the Missions invasion. The initial acts of barbarism gradually led to establishment of private properties, a movement that persisted along the southern Portuguese-Brazilian border until 1814. Alongside the appropriation of land, militias were formed, and expeditions were launched to exterminate the Minuano and Charrua peoples within their own territories. Due to these events, many Pampean widows and orphans emerged, who had been "domesticated" by their oppressors and were often distributed among the "settlers" or confined to *rancherios*.

Despite the colonial geopolitical disputes over territory, the authorities acted against the surviving peoples of the Southern Grasslands. In early 1803, the governor of Montevideo proposed a joint repression action to the interim governor of Rio Grande, Brigadier João Francisco Roscio. This order came from the Viceroy of the Prata River, who provided an initial military contingent. The reasoning was to "prevent the frequent robberies, deaths, and damages caused to the lives and properties of the subjects of His Catholic Majesty by the unfaithful Indians known as Charrua and Minuano, as well as a significant number of vagabonds and wrongdoers." As such, the governor of Montevideo requested his assistance so that the Portuguese commanders would also participate in pursuing them, following the Spanish officers in charge."

The brigadier pledged to "provide all the assistance and support necessary to prevent and suppress such disorders."[26] However, he warned the Portuguese Court that this partnership could also serve as a pretext for the Spanish to "reclaim the lands that were theirs before the treaties."

At that time, the Charrua *toldaria* led by Chief Gaspar was located in the territory of the Inhanduí Arroyo, a tributary of the Ibirapuitã Arroyo, within the agreed neutral area. Faced with repression, threats, and extermination attacks in the context of the Iberian disputes, he requested an audience with Governor Paulo José da Silva Gama in Porto Alegre in 1806. Chief Gaspar and his translator Agostinho Martins travelled over 500 km to the capital to meet with Governor Gama and his officials on July 18, 1806.

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[26] Official Letter of the [Viceroy of the State of Brazil], D. Fernando José de Portugal e Castro, to the [Secretary of State for the Navy and Overseas], Viscount of Anadia, João Rodrigues de Sá e Melo Meneses e Souto Maior. Rio de Janeiro, March 17, 1803. Lisbon: Overseas Historical Archive.

During the meeting, Chief Gaspar spoke in Guarani and was translated into Portuguese by Martins. The governor's correspondence, copies of which were sent to the Viceroy in Rio de Janeiro and the Secretary of the Navy and Overseas in Lisbon, reported that the "chief and his Charruas" were inhabitants of a place called Uarayaucay, south of the Ibicuy River, near the Portuguese outpost of Inhanduy.[27] He made himself understood through his interpreter, Agostinho Martins, stating that his name was D. Gaspar and that he was the *toldaria*'s chief. He informed his *toldaria* had "one hundred and fifty adult individuals," including "fifty armed individuals." Held between various forces in that border region, Chief Gaspar justified his proposal "to live in peace and tranquillity in the place where they were, under the protection and asylum of the Portuguese nation, with whom they desired to stay friends" as long as they were guaranteed that "his people, their wives, and children would never be pursued or harmed."

Paulo José da Silva Gama accepted, motivated by including additional 50 fighters in his jurisdictional troop.

The governor presented his justification to the Court, stating that the treaty with the Charruas aligned with the Portuguese policy of "conciliation and fair treatment of the indigenous people." He emphasized that this principle had guided his administration, taking full credit for the successful operation.

(i) I managed to have a Charrua chief named D. Gaspar come personally to this capital to beg for the protection of [His Majesty] and engage in the agreements that I deemed most advantageous. I am convinced that such a step will be regarded as extremely useful and important by all involved parties.

In the religious sphere, "these infidels, who have been buried in the blindness of paganism for so many centuries, will gradually be brought into the fold of our holy religion." However, the alliance had tremendous importance in that warlike conjuncture, as "these individuals are the most skilled in horse handling and the most experienced in this *Campanha* Grasslands." People who "are always to be feared" were being incorporated. The treaty with the Charruas was believed to hold its most significant relevance in geopolitics. The Portuguese were thus adopting a different tactical movement "from the Spaniards," who "eagerly desire to complete extinction" of the Charruas. Placing the Pampeans under Portuguese-Brazilian protection "in times of peace" would form "a formidable barrier against any surprises from our neighbours." And in times of war, their enlisted contingent would not bring "expenses to the Royal Treasury."

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[27] Modern-day Inhanduí Stream, a western tributary of the Ibirapuitã River. In the process of conquest, the "guard" or "outpost" referred to the establishment of a governmental entity on the frontier. Generally, it served as a starting point for the settlement, surveying, and distribution of land grants and the private registration of indigenous territories. The Guard of Inhanduí gave rise to the municipality of Alegrete.

All in agreement, the treaty with the Charruas was signed – with a copy given to Chief Gaspar – by "the governor of this captaincy, Paulo José da Silva Gama, accompanied by the prominent aristocracy of this town" of Porto Alegre.[28]

In this fashion, the Charruas were placed in military bodies, a similar framework imposed on the indigenous people of the Missions, especially the Guarani ethnicity. In the early decades of the nineteenth century, the cavalry regiment of the São Borja frontier consisted of 500 indigenous individuals and even had a marching band. Military units, regular or provisional, have historically served a dual purpose. They disrupted or weakened the indigenous people's connection to their traditional land occupations while integrating them as individuals into State defence corporations, often placing them in the subordinate layers of the emerging society and its experiences of racial mixing.

The first decades of the nineteenth century were harrowing for the indigenous peoples. The period was marked by widespread extermination, driven by the colonial and national states with underlying interests of privatization, exploitation, and enslavement. In the aftermath of the War of Conquest of the Missions, characterized by years of complete barbarism, Iberian interests sought to redefine territorial occupations in southern Brazil and the Prata River basin. The presence of the Portuguese Court in Rio de Janeiro in 1808 set in motion a series of events. Independence movements arose in the Prata River provinces in 1810, followed by Portuguese-Brazilian invasions in 1811. These invasions were largely influenced by the policies of José Artigas, who advocated for the rights of the Charruas and Minuanos. The occupation of the Eastern Bank in 1819, later annexed as the Cisplatin Province under the United Kingdom of Portugal, Brazil and the Algarves in 1821, further fuelled tensions. That led to a war with Argentina from 1825 to 1828, ultimately establishing the Oriental Republic of Uruguay through a Peace Treaty. Tragically, the formation of all these nation-states was marred by genocide against the indigenous peoples, perpetuated by ruthless elites.

In 1828, the presence of the *missioneiro* Guarani in the Pampa region was disrupted by continuous cycles of invasions and encroachments. The People-Chiefdoms' organization was lost, and the remaining population had to adapt to different roles, such as ranchers, small breeders, settlers, or labourers. Countless individuals acquired gaucho-like traits. During the Cisplatin War, the remaining organizational structures of the Missions were affected by the transfer of their contingents to the territories of the north-western Oriental Republic of Uruguay. In this emerging country, the *missioneiro* Guarani people played a crucial role as cattle farm workers. They made essential contributions to the modernization and exploitation of rural life, transforming the estates into centres of stable settlement. They possessed multiple skills and trades, excelling as artisans in rural and urban areas. They were masons, blacksmiths, carpenters, saddle makers, horsemen, shoemakers,

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[28] The official record of the treaty with the Charruas is documented in a protocol signed in Porto Alegre on July 18, 1806, and attached to the correspondence sent to the Viceroyalty of Brazil and the Court in Lisbon, including the letter from Governor Silva Gama of Rio Grande to Minister Sá e Melo on September 25, 1806. Lisbon: Navy and Overseas Archive.

coopers, weavers, musicians, painters, and decorators.[29] However, as time passed, they also gradually lost their identity as a people, facing a degradation process.

In the 1830s, groups of Pampeans still resisted in their *toldarias*. Some sought refuge in mountainous regions and inaccessible lands to establish cattle ranches and have access to hunting, gathering, and fishing areas. Nowadays, a vast bibliography deals with the extermination policies against the Charruas. The ethnocidal practices carried out by Fructuoso Rivera's government during and after the death of his nephew Bernabé are highlighted in this literature. The caudillo's explanation: "The criminal unruliness of these wild and degraded hordes and their recent and horrendous crimes left the government with no alternative but to attack and destroy them."[30]

The fate of the Charruas deported to France in 1833 is an emblematic example of the atrocities that occurred in 1831. They were handed over to the merchant François de Curel to be exhibited in the "Natural History of the Human Species" at the Champs-Élysées in Paris. The central figures in this tragedy were shaman Senaque, chief Vaimaca Perú, Micaela Guyunusa, and Laureano Tacuabé. Before their capture, Vaimaca Perú, in addition to the areas where his community lived in the Eastern Bank of Uruguay, also used to inhabit the Ibicuí River basin region in Rio Grande do Sul. Those Charruas never returned to America. They remained in Europe, showcased in circuses and other venues as barbaric specimens from the Pampa region.[31] A final image of this sorrowful history was portrayed in the melancholic drawing by Arthur Onslow (Fig. 7.6) (Prichard 1855).

While their vexation ritual was taking place in Europe, the *Toldería de los Charruas* still resisted at *Rincón del Yacaré Cururú*, Artigas Department, as documented in 1835 by the surveyor Manuel Eguía during his work for Colonel Servando Gomes. This *toldaria*, located at the intersection of the Quaraí and Yacaré Cururú rivers, was very close to the Charruas and Minuanos' last refuge in Rio Grande do Sul, in the highlands of the Ibirapuitã River headwaters. In 1841, the Viscount of São Leopoldo, concluding his effort to map the south of Brazil, marked this area as the "mountain range inhabited by the Charrua and Minuano Indians" (São Leopoldo 1841). This identification has been on maps since 1801. The indigenous resistance against extinction also underwent a topographical shift, as Pampa's peoples ultimately sought refuge in the mountains and forests of the Ibicuí River basin.

More broadly, one can consider that the twilight of the Pampeans as peoples of the Southern Grasslands unfolded in the 1840s. They would continue to be part of the mestizo current of the nineteenth century and, more rarely, through nuclear families that still identified themselves, albeit silently, by their ethnic identities.

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[29] "*El desenfreno criminal de las hordas salvajes y degradadas, sus recientes y horribles crímens, no habían dejado al Gobierno mas alternativas que la de atacarlas y destruirlas*." (Hilber 2019).

[30] A summary of this tragedy can be found in Portuguese in the subchapter "*Os últimos charruas*" (The last Charruas) in the aforementioned text by archaeologist and historian Klaus Hilber.

[31] The last of the Charruas (*Os últimos Charruas*), drawing by Arthur Onslow (Prichard 1855).

Fig. 7.6 The last of the Charruas (Os últimos Charruas). (Drawing by Arthur Onslow. Prichard, James Cowles. *History of Man*. London, 1855, Volume II)

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Part III

Diversity, Ecological Characteristics and Dynamics of *Campos Sulinos* Ecosystems

Chapter 8
Grassland Plant Community Composition and Dynamics: Disturbance as Determinants of Grassland Diversity

Bianca Ott Andrade, Luciana da Silva Menezes, Ilsi Iob Boldrini, Valério D. Pillar, and Gerhard Ernst Overbeck

8.1 Disturbance and Grassy Ecosystems

Disturbances, defined as events that remove plant biomass (Grime 2006), are the principal factors responsible for shaping the physiognomies and composition of grassy vegetation in environments where neither climate nor soil imposes limitations on tree growth (Bond and Keeley 2005; He et al. 2019; Bernardi et al. 2016). Due to the long evolutionary history of grasses in ecosystems with grazing animals and fire, plant communities in grass-dominated ecosystems harbor species that are adapted to various intensities and frequencies of these disturbances, either alone or

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in combination. We refer to these ecosystems as disturbance-dependent. When disturbances are intentionally excluded, the typical dynamics of these ecosystems will be disrupted. This often leads to biomass accumulation (Lezama et al. 2014), expansion of shrubs and trees (Müller et al. 2007, see also Müller et al. 2023, Chap. 16, this volume), and reduced productivity and diversity in the ecosystems (Westoby et al. 1989; Laycock 1991).

The responses of grassy vegetation to disturbances are diverse and multifaceted. At the species level, these responses depend on morphological and physiological characteristics that enable species to either avoid (e.g., by reducing the probability and intensity of defoliation) or tolerate (e.g., mechanisms facilitating plant regrowth following defoliation) a disturbance event (Díaz et al. 2006; Fischer et al. 2019). At the community level, the response to disturbances is expected to be influenced by primary productivity and dominance, as well as the role of disturbances over evolutionary periods (Milchunas et al. 1988; Cingolani et al. 2005; Koerner et al. 2018). In highly productive plant communities, disturbances typically reduce the dominance of a few competitive species, thereby promoting the formation of spatial heterogeneity and enabling more species to coexist (Lezama et al. 2014; Yuan et al. 2016).

In Brazil, disturbance-prone grassy ecosystems, such as grasslands and savannas, originally extend over 27% of the territory (Overbeck et al. 2022). Even though 46% of these ecosystems have already been converted to other uses, this clearly demonstrates that, when it comes to natural ecosystems and biodiversity, Brazil has more than just forests, although this fact is not widely recognized by the public. Different savanna physiognomies, which are prevalent in the Cerrado region but also found in the Amazon, Caatinga, and Atlantic Forest regions, constitute the main part of these open ecosystems (Ribeiro and Walter 2008). Disturbances, especially fire, play a key role in shaping the physiognomies, species composition, and dynamics of these savannas (Furley 1999; Rodrigues et al. 2021). Grasslands and other communities dominated by low-growing plants can also be found in higher parts of the coastal mountain range in eastern Brazil, as well as on mountaintops within the Cerrado and other regions (see Overbeck et al. 2022 for a synthesis). The South Brazilian grasslands, known as *Campos Sulinos* (see Box 8.1; Pillar et al. 2009; Pillar and Lange 2015; Overbeck et al. 2018; Hasenack et al. 2023), are true grasslands, where grasses are the most abundant group of species. They do not contain tall woody plant component typical of tropical savannas. These grasslands occupy large portions of the Brazilian Pampa (IBGE 2019), located in the southern half of Rio Grande do Sul state. They also form mosaics with forests in the highlands of the southern part of the Atlantic Forest region, which encompasses northern Rio Grande do Sul state and the states of Paraná and Santa Catarina. This extensive region of grasslands is home to an enormous biodiversity. For the Pampa region alone, there are 3,642 species of vascular plants, with 2,105 of them relying on grasslands as their primary or sole habitat (Andrade et al. 2023). Although an exact number is unavailable for the *Campos Sulinos* region as a whole, we can reasonably expect around 4,100 grassland plant species (I. Boldrini, unpublished data).

Box 8.1: Disentangling a Bestiary of Names for the Campos Sulinos

The term *Campos Sulinos* refers to the grasslands found in two phytogeographic regions, namely the Atlantic Forest and Pampa biomes, as classified by IBGE (2019) in the Brazilian biome classification. Similarly, Morrone (2001) classifies vegetation into two different provinces and subregions (in parentheses): *Pampa* (*Chaqueña*) and *Bosque de Araucaria angustifolia* (*Paranaense*). The grasslands within the Atlantic Forest region (also known as *Campos do Planalto das Araucárias* in Portuguese; 22.5°S–30°S, 48.5°W–54.5°W) have different regional names. The northeast part of Rio Grande do Sul (RS) is commonly referred to as highland grasslands (*Campos de Cima da Serra*) due to their altitudinal range of 600–1,200 m a.s.l. In Paraná state, in the extreme north of the region and in transition with savanna ecosystems, grasslands are known as *Campos Gerais* (Overbeck et al. 2022).

The Pampa grasslands are part of a continuous region that covers vast plains, with only low mountain ranges, in central-eastern Argentina, Uruguay, and the southern part of Brazil (27.5°S–39°S, 50°W–67°W), known as *Río de la Plata* grasslands (RPG) (Soriano et al. 1992; Andrade et al. 2018). Soriano et al. (1992) identify two sub-regions within the RPG based on floristic similarities: the *Campos* (Southern Rio Grande do Sul and Uruguay), further divided into northern and southern *Campos* (*Campos del Norte* and *Campos del Sur* in Spanish, with the Brazilian portion being part of '*Campos del Norte*'), and the *Pampa* (part of provinces of the eastern part of Argentina; subdivided into Rolling Pampa, Inland Pampa, Southern Pampa, Flooding Pampa, and Mesopotamic Pampa).

In its description of the dominant ecosystems in the region, the Brazilian Institute of Geography and Statistics (IBGE 2019) does not use the term grassland (*campo* in Portuguese), but instead refers to the grassland ecosystems in southern Brazil as "steppe" (*estepe* in Portuguese). However, this term seems inappropriate as it usually refers to semi-arid grasslands (with rainfall of 250–500 mm) under temperate climates (Overbeck et al. 2007), which is clearly not the case in southern Brazil. A small part of the region, located in the extreme west of Rio Grande do Sul state and regionally known as *Espinilho*, characterized by the presence of a disjunct tree layer of *Prosopis affinis* (Marchiori and da Silva 2011), is referred to by IBGE (2019) as "steppe-savanna" (*savana estépica* in Portuguese). However, we also discourage the use of this term as the climate in the region is neither that of a savanna nor a steppe, even though, in physiognomic terms, the vegetation could be called 'savanna-like' (*savanoide* in Portuguese).

The term "*Pampas*", ending in s, is commonly used in music, art, and poetry, but it often lacks a defined geographic region and can refer to part or all of the RPG. In Uruguay and Argentina, the Spanish term "Pastizales" is used for grassland ecosystems (e.g., Morrone 2001).

Fig. 8.1 Cultural landscapes of the *Campos Sulinos* region, including heritage sites and traditional livestock management practices with domestic animals. São Miguel das Missões, RS, Brazil and its surroundings. (Photographs courtesy of Bianca Ott Andrade)

Since the European colonization of the region, the *Campos Sulinos* grasslands have been used for extensive cattle grazing. As a result, they can now be considered a cultural landscape (Fig. 8.1), even though this term is not widely used in Brazil. Livestock production in the region continues to rely largely on natural grasslands and traditional production systems (Modernel et al. 2016). In addition to providing meat, wool, leather, and other animal products, these grasslands offer various ecosystem services of local and global importance. These services include soil stabilization, water filtering, carbon storage, habitat protection for biodiversity, watershed regulation, food and fiber production, cultural services, and improved living conditions for grazing animals (Tittonell 2021). The provision of these services depends – as grasslands in general – on disturbance regimes. Therefore, understanding how disturbances in grasslands impact plant diversity and ecosystem functioning is crucial for preserving, managing, and restoring these grasslands in a changing world. In this chapter, we discuss the main disturbances that influence vegetation composition, structure, and functioning of *Campos Sulinos* grasslands. We begin with an overview of the ecological context of these grasslands and the main grassland types found in the region. Subsequently, we explore the different types of disturbance and their spatial and temporal effects. We also discuss the nuanced boundary between disturbance and degradation, as well as practical applications at various ecological scales.

8.2 *Campos Sulinos* Grasslands

8.2.1 Climatic Setting and Disturbance History

In southern Brazil, tree growth is not limited by general soil or climatic constraints, although drier periods can occur, especially in summer. The absence of trees in large parts of the landscape, known as the “Pampa problem” (Troll 1968), had puzzled researchers until recently. Presently, researchers working in the region acknowledge the prominent role of disturbances in maintaining open grasslands, as demonstrated by integrated modeling of rainfall, grazing, and fire (Bernardi et al. 2016). Grasslands and forest coexist in the landscape in varying proportions. The *Campos Sulinos* grasslands span a precipitation gradient from 1,200 to 2,700 mm and an average temperature gradient from 13 to 22 °C (Fig. 8.2; Alvares et al. 2013). Grasslands dominate the landscape below 1,660 mm of precipitation, to the south and southwest, while forests prevail above 1,800 mm, toward the north. Between 1,660 and 1,800 mm, both ecosystem types occur in more equal proportions (Fig. 8.2). However, the precipitation levels across the entire region allow for tree growth and forest development. Here, we propose a conceptual model, in which disturbance plays a key role in explaining the grassland-forest gradient observed in southern Brazil, particularly the co-occurrence of both vegetation types in the central portion. We interpret the x-axis as a disturbance spectrum, explained by the recurrence of disturbance, light competition, and topographic heterogeneity (Fig. 8.2; see also Burke et al. 1998). The frequency of disturbance is a crucial factor in determining the vegetation composition of the landscape, with grasslands, grassland-forest mosaics, and forests occurring in a sequence of higher to lower disturbance recurrence (Blanco et al. 2014). According to Engel et al. (2023), grassland ecosystems under higher temperature and precipitation levels support greater productivity, where tall and acquisitive species (i.e., those with greater specific leaf area) are favored due to their superior ability to use the available resources. Similar results are observed along a forest and grassland-forest gradient (Del Grosso et al. 2008).

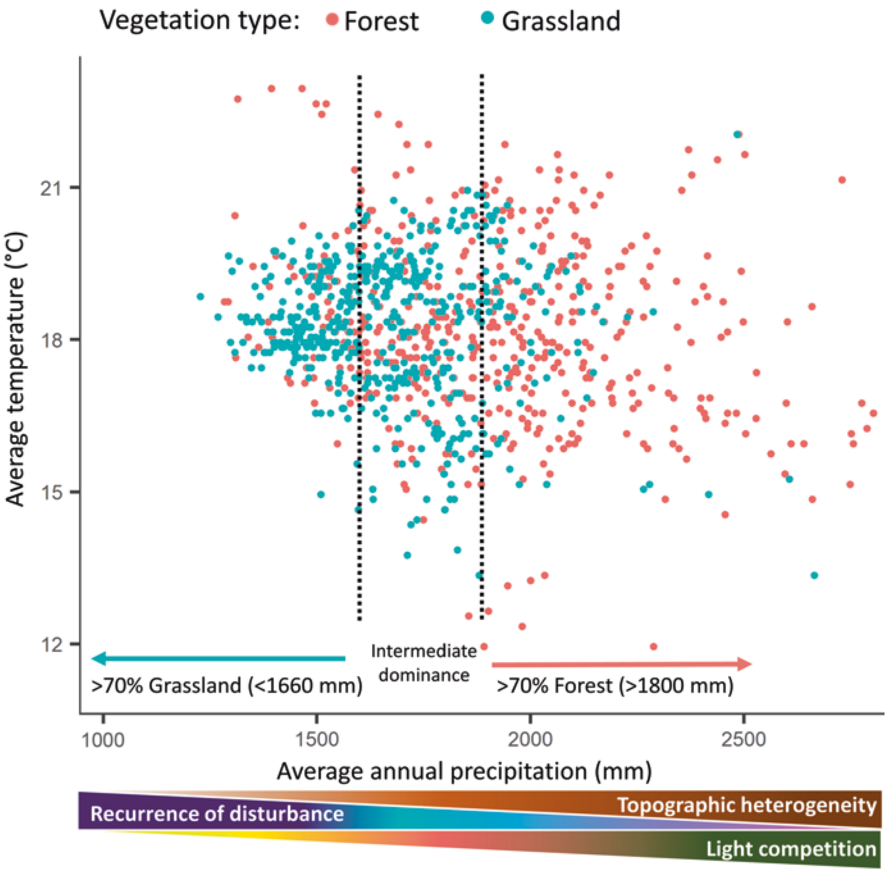


Fig. 8.2 Conceptual model depicting the relative importance of grazing and fire disturbance on the occurrence of grassland and forest ecosystems along a precipitation and temperature gradient in southern Brazil. We interpret the x-axis as a disturbance spectrum, which is explained by the recurrence of disturbance, light competition, and topographic heterogeneity. To build this figure, we randomly selected a thousand random points from known vegetation types in southern Brazil, with 500 points representing each grassland and forest vegetation. (MapBiomas v.7, Souza et al. 2020). Temperature and precipitation data for these points were obtained from WorldClim. (Fick and Hijmans 2017)

Additionally, as demonstrated by Blanco et al. (2014), topographic heterogeneity is an important factor contributing for the long-term coexistence of forest and grassland in the landscape. It results in increased local spatiotemporal variability, impacting seed dispersal, fire spread, and microclimatic variations.

Fire and grazing have been present in the *Campos Sulinos* long before the arrival of human populations in the region (Baggio et al. 2021; Pivello et al. 2021; Paruelo et al. 2022). The effects of these disturbances on the plant community will be discussed in detail in Sect. 8.3. However, when considering the role of past disturbances, it is important to acknowledge that the frequency and intensity of these disturbances were likely different compared to the current regimes, which are heavily influenced by human land use. Palaeoecological studies analyzing pollen composition in peat bogs provide information on the fire regimes over the past millennia. Fires were relatively rare during glacial periods, but an increase in the concentration of carbonized particles is observed in the South Brazilian highland region between 11,500 and 7,400 cal yr. BP, likely associated with the arrival of human populations (Behling and Pillar 2007; see also Behling et al. 2023, Chap. 4, this volume). These changes may also reflect climatic changes and altered grassland productivity, which was lower during periods of lower temperature and precipitation levels. On the other hand, evidence of grazing by megafauna that inhabited the grassy ecosystems of South America extends much further back in time, as indicated by the fossil record. Grazing by this megafauna persisted until the end of the Pleistocene, when their extinction coincided with climatic shifts and the arrival of human populations (Barnosky et al. 2016; Croft et al. 2020; Prates and Perez 2021). While it is impossible to quantify the effects of past disturbances, the legacy of these disturbances is evident in the adaptations of plants and animals to fire and grazing (Archibald et al. 2019; Pivello et al. 2021), indicating that both processes have acted as evolutionary forces.

8.2.2 Current Classification of Campos Sulinos *Grasslands*

Early naturalists and researchers primarily classified grasslands in southern Brazil based on their physiognomy. Even today terms such as *campo limpo* (meaning "clean grassland") and *campo sujo* (literally translating to "dirty grassland," indicating the presence of shrubs) are commonly used. Until recently, there was no classification based on vegetation composition, as studies were often limited to single or a few locations and did not provide a comprehensive coverage of the entire region. However, a recent study by Andrade et al. (2019) addressed this gap by examining a large sample of sites spanning the entire *Campos Sulinos* region. They identified three main grassland types, namely Pampa grassland, South Brazilian highland grassland, and South Brazilian coastal grassland (Fig. 8.3). Additionally, they distinguished ten grassland subtypes within this classification, which were primarily based on plant composition and reflected the underlying geological, geomorphological and pedological aspects of the region.

8.2.2.1 South Brazilian Highland Grasslands

The South Brazilian highland grasslands are located in the southernmost portion of the Atlantic Forest, in the states of Santa Catarina and Paraná as well as northeastern Rio Grande do Sul (Fig. 8.3). Within this region, the grasslands form mosaics with forest ecosystems, particularly *Araucaria* forests, and they transition to the Cerrado biome in the north. The climate in the region is characterized as oceanic,

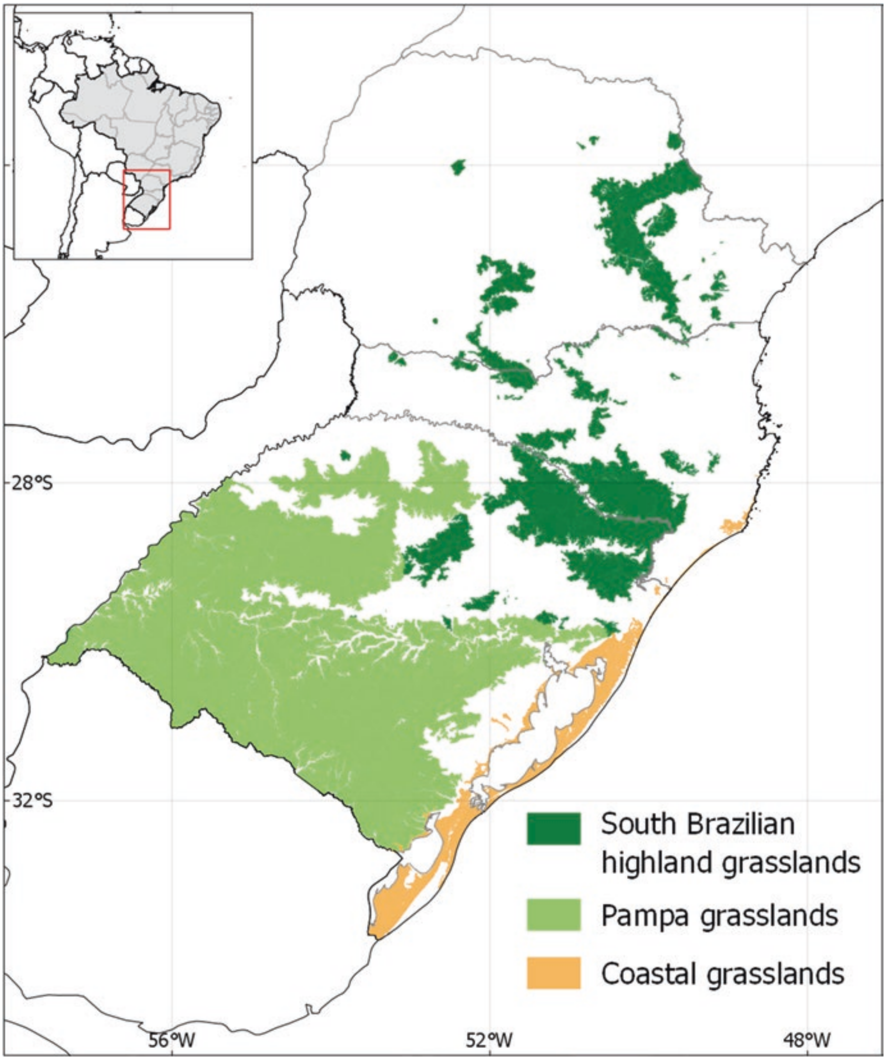


Fig. 8.3 Geographical location of the *Campos Sulinos* in Brazil along with the three main types of grassland vegetation types found in the region: Pampa grasslands, South Brazilian highland grasslands, and Coastal grassy ecosystems

with temperate summers and no distinct dry season (classified as Köppen's Cfb climate). The mean annual temperature ranges from 12 to 16 °C, and average annual precipitation varies from 1,300 to 2,200 mm (Alvares et al. 2013). Meteorological frost events occur from 10 to more than 27 days per year (Alvares et al. 2018). The soils in the region originate from volcanic rocks such as basalt, rhyolite, and rhyodacite. The combination of low temperatures and high rainfall contributes to greater accumulation of organic matter in the soil. Furthermore, the complexation with ionic aluminum enhances the stability of organic matter (Silva et al. 2008). For further information on climate and soils, see also Hasenack et al. (2023, Chap. 6, this volume). The vegetation in the South Brazilian highland grasslands is characterized by the predominance of tussock grasses with C4 photosynthetic pathways. Indicator species for these grasslands as a whole include *Schizachyrium tenerum* (C4 grass), *Dichanthelium sabulorum* (C3 grass), *Baccharis crispa*, *Chaetogastra gracilis* (Andrade et al. 2019). Other typical species found in this region include *Andropogon lateralis* (C4 grass), *Aristida flaccida* (C4 grass), *Calea phyllolepis*, *Eragrostis polytricha* (C4 grass), *Paspalum maculosum* (C4 grass), *Paspalum plicatulum* (C4 grass), *Paspalum polyphyllum* (C4 grass), and *Piptochaetium montevidense* (C3 grass) (Andrade et al. 2019).

The patches of grasslands intermingled with forests in the highland grassland region are remnants of drier and cooler climates (Arruda and Schaefer 2020; Asevedo et al. 2020). The current humid climate developed only at 1.5 ka BP (Bauermann and Fett Junior 2014). During glacial periods, the grasslands expanded, and during interglacial periods they contracted, allowing for their replacement by forest ecosystems. For example, during the dry and cold last glacial maximum (LGM; approximately 29–11.7 ka BP), the highland grasslands expanded approximately 250 km to the north, occupying areas that were formerly covered by deciduous forest (Arruda et al. 2018; Maksic et al. 2022). These vegetation shifts during glacial and interglacial periods had an impact on species gene flow, which could have been repeatedly interrupted and then re-established. The high species richness (Boldrini 2009a) and high levels of endemism (Külkamp et al. 2018) are results of these processes.

Under the current climate, characterized by cold winters with frost events, the highland grasslands have a low carrying capacity of grazing animals during the winter when C4 grasses produce minimal biomass. As a result, they have traditionally been managed with low stocking rates throughout the year, allowing for the accumulation of standing dead biomass during the more productive summer. Consequently, mild surface fires, occurring annually or biennially (Silva and Andrades-Filho 2021), are commonly used in the region to remove dead biomass and promote the regrowth of grasses and palatable herbaceous forage biomass. This practice likely originated with the occupation of indigenous communities (Behling and Pillar 2007). When fire or grazing is excluded, tall tussock grasses become dominant (e.g., *Sorghastrum* sp., Andrade et al. 2016), and shrub encroachment and forest expansion may take place (see Müller et al. 2023, Chap. 16, this volume).

8.2.2.2 Pampa Grasslands

The Pampa grasslands, located in the southern half of Rio Grande do Sul state (Box 8.1, Fig. 8.3), covered an area of 8.4 Mha in Rio Grande do Sul state in 2001. However, 24% of this area has been lost in the past 20 years (Baeza et al. 2022). While the Pampa grasslands share a large number of species with the South Brazilian highland grasslands, their plant communities differ in terms of floristic composition

(Andrade et al. 2019). Indicator species include rhizomatous/stoloniferous C4 grasses such as *Paspalum notatum* and *Axonopus affinis*, the caespitose *Setaria parviflora* (C4 grass) and *Steinchisma hians* (C3 grass), and forbs like *Gamochaeta americana* (Andrade et al. 2019). Other common species in the Pampa include *Dichondra sericea*, *Eragrostis neesii* (C4 grass), *Evolvulus sericeus*, *Piptochaetium montevidense* (C3 grass), *Richardia humistrataI*, *Richardia stellaris*, *Nassella* spp. (C3 grass), and *Adesmia* spp. (Andrade et al. 2019). The Brazilian Pampa harbors the largest number of endemic species known in the *Río de la Plata* grasslands, with 309 endemic species out of a flora composed of 3,642 vascular plant taxa (Andrade et al. 2023).

Compared to the South Brazilian highland grasslands, the soils in the Pampa grasslands – originated from igneous plutonic, metamorphic, and sedimentary substrates – are more diverse (Streck et al. 2008). Also, precipitation levels in the Pampa are lower, ranging from 800 to 1200 mm. While there is no pronounced dry season, some regions may experience annual hydric deficits with summer droughts. The climate is of a Cfa type according to Koppen's classification (Alvares et al. 2013). Meteorological frost events range from 1 to 18 days per year in the region (Alvares et al. 2018). Additionally, extreme climatic events during La Niña phases of the ENSO cycle can prolong and intensify the drought period (Matzenauer et al. 2017), potentially limiting forest expansion in the Pampa. Nonetheless, the prevalence of grasslands is considered to be primarily a result of current land use and disturbance regimes rather than climate (Bernardi et al. 2016).

Grazing has historically shaped the physiognomy of the Pampa grasslands. During the Pleistocene, large grazers or mixed-diet animals, such as horses (*Equus neogeus*) and mastodonts (*Notiomastodon platensis*) (França et al. 2015; Lopes et al. 2022), lived in the Pampa. With a diet composed mostly of C4 species, horses, for example, inhabited grass-rich open landscapes in the region (França et al. 2015).

8.2.2.3 Coastal Grassland

Coastal grasslands have developed on recent sedimentary soils (Fig. 8.2). The substrate in the coastal region of southern Brazil, primarily in Rio Grande do Sul, was formed by progressive/regressive movements of the coastline during the Late Quaternary, approximately 400 kyr BP (Dillenburg et al. 2009). Local variations in soil types and humidity are important factors shaping the grassland plant communities (Boldrini et al. 2008; Menezes et al. 2016). Lagoonal and riverine depositional processes have formed soils rich in clay and organic matter, classified as Histosol, Gleysol, and Planossol soil types (Santos et al. 2018). These soils have poor drainage conditions and allow for the growth of species adapted to intermittent flooding. Indicator species for the coastal grassland region as a whole include *Steinchisma hians* (C3 grass) and *Lobelia hederacea* (Andrade et al. 2019). On a regional scale, different types of grassland communities can be recognized and classified based on humidity levels. Marsh vegetation is characterized by high levels of soil organic matter content and groundwater level close to the surface, while well-drained open and shrub grasslands vary based on soil characteristics, vegetation height, and bare soil coverage (Silveira et al. 2022). On slightly higher relief, the soils in the coastal grasslands have predominantly developed on former dunes. These grasslands experience drier soil conditions, and the main soil types are Plinthosols, Podzols, and Leptosols (Santos et al. 2018). The drier coastal grasslands are characterized by the abundance of prostate and rhizomatous C4 grasses, such as *Axonopus* aff. *affinis* and *Stenotaphrum secundatum*. Common species with high palatability and nutritional value for livestock include *Ischaemum minus* (C4 grass, Boldrini 2011) and Fabaceae species like *Desmodium barbatum* and *Indigofera sabulicola* (Boldrini 2009b). Insectivorous species such as *Drosera* spp. and *Utricularia* spp. indicate nutrient-poor conditions.

Similar to the other ecological units of the *Campos Sulinos*, cattle raising is an important economic activity in the coastal grasslands. While these grasslands harbor species of good forage quality, overgrazing appears to be a problem in the region, indicated by high levels of bare soil observed in grazed areas (around 15% according to Menezes et al. 2016), which is considered a sign of degradation (Boldrini et al. 2008). However, cattle are not the only herbivores in the coastal grasslands. Burrowing rodents, known as *tuco-tucos*, dig furrows to hide and feed on plant roots (Galiano et al. 2014). In the process, *tuco-tucos* can cause significant local impacts, uprooting plants and leaving up to 61% of the soil uncovered (Galiano et al. 2014). The extent to which bare ground in coastal grasslands is due to overgrazing or is an intrinsic characteristic of unstable soils remains an open question.

8.3 Complexity of Disturbances: Legacies, Modulating Factors, Spatial and Temporal Mosaics

Vegetation disturbances (Fig. 8.4) are complex events. Distinct disturbance regimes, which encompass the type, frequency, seasonality, intensity, and extent of disturbances, have specific effects on plant community structure and composition (Foster et al. 1998). Legacies of past events can take the form of physical and biological items or substances left behind after the disturbance event (e.g., ashes from a burn or cattle droppings after grazing) or as filtered information within the community (e.g., species selection with traits to overcome the disturbance) (Johnstone et al. 2016). Legacies from one disturbance may promote or prevent the occurrence of subsequent events (Foster et al. 1998), such as the resprouting of fresh biomass that attracts grazers after a fire event. Conversely, grazers consume plant biomass, preventing the accumulation of dry fuel material and thus reducing the occurrence of fire.

The outcomes of disturbances are influenced by their frequency and intensity. Frequency refers to the return interval of a disturbance event (Jentsch and White 2019) and can vary greatly depending on the disturbance type. For instance, in the *Campos Sulinos* grasslands (Overbeck et al. 2007), burning typically occurs at intervals of 2–5 years, whereas grazing occurs year-round in the region, primary as continuous grazing, although there is occasional rotational grazing (Boavista et al.

Fig. 8.4 Disturbances that influence biodiversity in the *Campos Sulinos*: (**a**) grazing by livestock in Aceguá, RS; (**b**) prescribed fire in Saint-Hilaire Municipal Park, Viamão, RS; grazing by wild fauna, such as (**c**) the brown brocket deer (*veado-catingueiro*, *Mazama gouazoubira*) in São Joaquim National Park, Santa Bárbara, SC, or (**d**) greater rhea (*Rhea americana*) in Santana do Livramento, RS; bioturbation caused by (**e**) armadillo (in Santiago, RS) and (**f**) arthropods (in São Francisco de Assis, RS) when burrowing nests or galleries. (The photographs are courtesy of Valério Pillar (**a**), Juliana Schaefer (**b**), Martin Grings (**c**, **d**) and Fernando Furquim (**e**, **f**))

2019; Paruelo et al. 2022). Fire intensity is defined as the amount of energy released during burning (Keeley 2009), while grazing intensity is typically represented by the ratio between the total animal living weight and the area of grazing management (measured by stocking rate or density) over a specific period of time (Allen 2011). However, grazing intensity can be more adequately measured by considering the forage allowance, which is the ratio between the total available forage and the total animal living weight in the area of grazing management (Sollenberger et al. 2005). In addition to the temporal scale, the spatial scale matters and influences plant community composition at the landscape scale. In the following sections, we delve into the effects of the main disturbance drivers in the plant communities of the *Campos Sulinos*, namely grazing and fire. We discuss not only their effects on vegetation and the distribution of different plant functional types but also the implications for grassland management.

8.3.1 Grazing by Domestic Animals

As mentioned earlier, megafauna and other herbivores were important components of the *Campos Sulinos* grasslands in the past. However, today, most of the grasslands in the region are grazed by domestic animals, primarily cattle but also sheep and horses. These domestic animals have taken over the ecological niches left vacant by the extinction of large herbivores. Different plant species exhibit varying levels of resistance to grazing, which is determined by their ability to evade grazing (avoidance; Fig. 8.5a–c) and regenerate after defoliation (tolerance; Fig. 8.5d–f). Grazing encompasses defoliation, trampling, and nutrient deposition through feces and urine (Lezama and Paruelo 2016). Defoliation and trampling are the main processes influencing vegetation composition and dynamics, which we will discuss further below. Nutrient deposition has a localized impact on the plant community, as droppings and urine are mostly concentrated around animal trails and watering areas (Schrama et al. 2013). However, there are additional effects, including seed dormancy being overcome by passage through the intestinal tract, and seed dispersal facilitated by animals (Minervini-Silva and Overbeck 2021; Azevedo et al. 2023). The effects of grazing vary among herbivore species (Carvalho and Moraes 2005), and domestic grazers certainly influence the plant community differently than extinct large herbivores. It is worth noting that grazing by horses is an exception, as the modern horse is closely related to the native *Equidae* that once roamed the *Campos Sulinos* region (Croft et al. 2020). In fact, DNA evidence (Orlando et al. 2008) has shown that *Equus neogeus* and the domesticated horse (*Equus caballus*) should be recognized as conspecific.

The response of plant communities to different grazing intensities has been extensively studied in the *Campos Sulinos*, particularly in a long-term experiment conducted at the UFRGS Agronomic Experimental station in Eldorado do Sul, RS. This experiment has been managing different paddocks with varying forage allowances for over 35 years (Carvalho et al. 2019). Additionally, several sites of the Long-Term Ecological Research (LTER) *Campos Sulinos* have contributed to the understanding of grassland responses to grazing (see Box 8.2; Ferreira et al. 2020). Forage allowance is a key factor in modulating the impacts of grazing on vegetation. Under high forage allowance (low grazing intensity), cattle tend to selectively graze more palatable plants and ignore less attractive ones. Consequently, less palatable species dominate the plant community. These are typically slow-growing species, including many hard-leaved and tall-growing bunchgrasses and perennial herbs with a resource-conservative strategy (Díaz et al. 2006; Fischer et al. 2019; Ferreira et al. 2020), such as *Andropogon lateralis*, *Aristida* sp., and *Sporobolus indicus*,

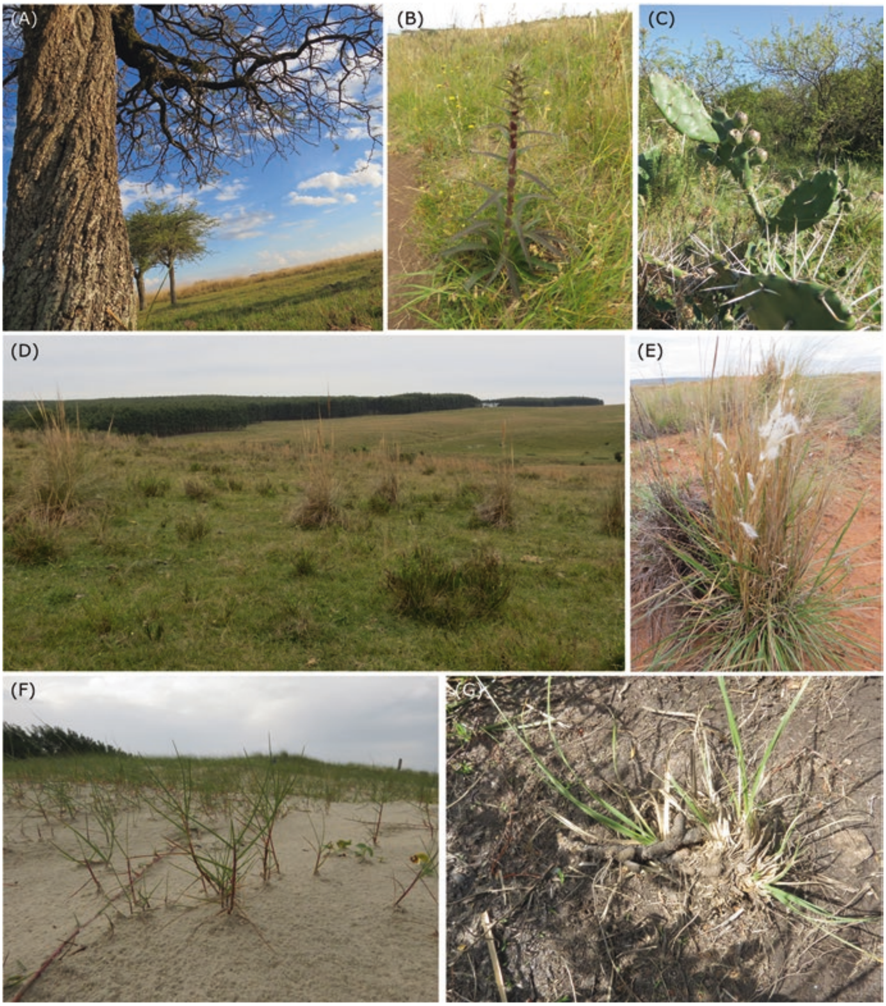


Fig. 8.5 Plant traits that contribute to avoidance and resistance to disturbance effects. In (**a**), the deposition of lignin in the bark of *Prosopis affinis* enables grazing and fire avoidance. Mechanical deterrents, such as thorns in *Eryngium horridum* (**b**) and *Opuntia elata* (**c**), prevent grazing animals from consuming these species. Moving on to (**d**–**g**), different strategies adopted by herbaceous plants in relation to bud protection are observed, which facilitate rapid regrowth after a disturbance event. Tussock grasses such as *Saccharum angustifolium* (**d**) and *Andropogon selloanus* (**e**) have buds protected from fire at the base of the plant. Additionally, tussock grasses often have leaves of low palatability, leading grazing animals to avoid them, thus creating the typical two-layer structure of grasslands (**e**). Rhizomatous grasses like *Panicum racemosum* (**f**), commonly found in harsh conditions of mobile coastal dunes, and *Paspalum notatum* (**g**) also have the ability to resprout after biomass loss. However, in the case of *P. notatum*, buds located at the soil surface are vulnerable to fire. (Photographs by Bianca Ott Andrade)

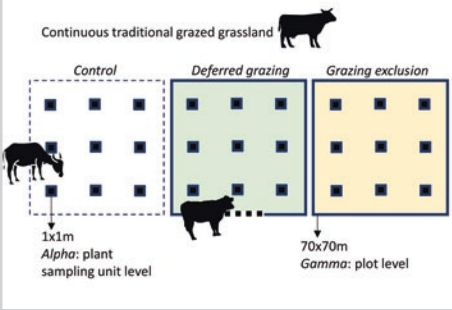
Box 8.2: Campos Sulinos Long-Term Ecological Research (LTER)

In 2010, the *Campos Sulinos* LTER experiment was established in response to a conservation policy that promoted fire suppression and grazing exclusion in grassland protected areas in Brazil. The purpose of the study was to assess the effects of reducing or excluding grazing on plant and animal diversity over space and time. The experiment used a randomized block design with three treatments: (i) continuous traditional grazing [control], (ii) grazing exclusion, and (iii) deferred grazing, which represented an intermediate approach between the first two treatments. Here, we present the results from the first 4 years of the experiment (for more details, refer to Ferreira et al. 2020).

Both exclusion and deferred treatments resulted in an increase in vegetation height, vegetation biomass, and standing dead biomass over time compared to the control treatment. The reduction in grazing intensity affected the functional composition and diversity of plants over time. Exclusion and deferred treatments led to a decrease in the dominance of prostrate species, followed by a rapid homogenization of vegetation structure toward the dominance of taller species. Regarding diversity, there was an initial increase in plant taxonomic diversity at all spatial levels (1 m^2 plot for alpha, and 70 m^2 plot for gamma diversity) in the first year. This positive effect lasted longer, particularly for beta and gamma diversity, in the deferred grazing. However, it became non-significant and negative in the following years for the grazing exclusion treatment.

The effects of both deferred grazing and grazing exclusion treatments cascaded through the animal communities inhabiting the grassland vegetation, resulting in an overall increase in the richness of arthropod high-taxa and the abundance of individuals from different trophic levels. These included herbivores such as true bugs (Hemiptera) and flies (Diptera), as well as predators such as spiders (Araneae). The presence of arthropods in the vegetation was favored by the increase in biomass, which provided food resources, shelter, and breeding sites. However, soil arthropod richness and abundance were not significantly affected by the treatments.

As practical implications of this study, Ferreira et al. (2020) suggest that conservation of grasslands in *Campos Sulinos* should maintain patches of both intensive and alleviated levels of grazing management (as well as other disturbances such as fire), rather than completely excluding grazing.



Deferred vs. Continuous grazing

Deferred grazing vs. grazing exclusion at the back (bush line)

Photos by Ana Boeira Porto

which accumulate senescent material (Cruz et al. 2010). Additionally, shrubs that are sensitive to trampling can establish at very high forage allowance, including species from the Asteraceae family like *Baccharis dracunculifolia*. These shrubs possess characteristics leading to grazing avoidance, such as hard leaves and woody biomass (Streit et al. 2022). Conversely, at low forage allowance (high grazing intensity), tall grasses and shrubs cease to exist or experience a drastic reduction in cover within the plant community, unless they are so unattractive and rejected by grazing animals (e.g., very spiny plants, toxic plants). However, even in such cases, they may suffer from trampling at high intensities. High levels of grazing will select for more grazing tolerant plants due to their ability to grow quickly (Fischer et al. 2019). These species are characterized by their resource acquisition strategy (Díaz et al. 2006) since they can rapidly mobilize resources and invest in the growth of aboveground biomass, reproductive structures, and/or reserve structures. Examples in the *Campos Sulinos* include broadly distributed prostrated grasses such as *Paspalum notatum, Paspalum paucifolium*, and *Axonopus affinis* (Cruz et al. 2010; Streit et al. 2022).

Thus, grazing selects plant traits to tolerate disturbances at intraspecific and community level (Díaz and Cabido 2001). This selection seems to be more related to a negative selection (exclusion) of species that perform poorly under grazing disturbance. In a simulated grazing experiment, tussock grasses (resource conservative species) reduced their abundances under higher clipping intensities, while other plant life forms did not change their abundances regardless of clipping intensities (Jorge et al. 2022). Resource acquisitive species further benefit indirectly from grazing, as they take advantage of the reduction of biomass from dominant species and canopy opening. Interestingly, the plant traits that confer grazing tolerance are the same that characterize plants as more palatable (Díaz and Cabido 2001). For example, tender leaves grow faster (Poorter et al. 2009), and low fiber leaves are preferred by grazers due to better digestibility (Queiroz et al. 2000). Rapid growth is considered a characteristic of grazing tolerance due to an overlap between plant traits related to plant community response to grazing (response traits) and traits that influence forage selection by grazers (effect traits) (Blanco et al. 2007). In other words, the resulting plant community after grazing is more palatable and attractive to grazing compared to the surrounding ungrazed patches, creating positive feedback cycles.

Under intermediate stocking rates, grazing is not homogenous, as herbivores preferentially graze on more palatable plants and create patches of ungrazed sites (Ferreira et al. 2020). For example, plants with mechanical deterrents (e.g., thorns in *Eryngium horridum* (Fig. 8.5**b**), inflorescence awns in *Aristida laevis*, prickles in *Smilax campestris*) and biochemical compounds that make them less palatable (e.g., *Baccharis coridifolia*; Rissi et al. 2005) or even toxic to cattle (e.g., ragworts *Senecio* sp.; Antoniassi et al. 2011) will be avoided by grazers. Other species tend to be more tolerant to grazing, such as prostate species such as *Axonopus affinis* or *Paspalum notatum* (Fig. 8.5**f–g**), because they are able to keep their potential sites of regrowth (buds or meristems) close to the soil, inaccessible to animals, compared to bunchgrasses (e.g., *Andropogon lateralis*, *Sorghastrum pellitum*) (Fig. 8.5**d–e**). Across larger areas, the result of intermediate stocking rates will be the formation of grazed/ungrazed patches, promoting biodiversity of plants and associated taxa in grasslands in a typical two-layer structure with low grazing lawns, formed by prostrate species, and taller clumps of tussocks and other less palatable species in between (Fischer et al. 2019; Ferreira et al. 2020).

Understanding vegetation responses to different grazing regimes has important implications for rangeland management, conservation, and restoration. Changes in frequency and intensity of grazing may promote species recovery and ex situ conservation, habitat conservation, restoration and rehabilitation, climate mitigation, among other outcomes commonly listed by land managers and ranchers. An example is the implementation of rotational grazing instead of the traditional continuous grazing in large areas. Under rotational grazing, the pasture is divided into smaller paddocks and animals are transferred between them, allowing greater control of grazing time and amount of forage offered to the animals. The grazing intensity will be momentarily higher, in a short time interval, and after that the vegetation will be able to recover during a period without grazing. Boavista et al. (2019), who analyzed changes in composition, diversity, and biomass production after implementing rotational grazing management in grassland communities that were formerly under continuous grazing management, observed an increase in species richness and more uniform species growth over a period of 6 years due to reduced selective grazing. Longer periods of exclusion from grazing can be especially beneficial for restoring overgrazed sites, where the plant community has been intensively grazed for an extended period without sufficient recovery periods (Mysterud 2006). In the *Campos Sulinos* region, overgrazing is a common problem that often results in plant communities characterized by very short grazing lawns, low productivity, high dominance of prostrate grasses, and the presence of ruderal species. Fedrigo et al. (2017) presented encouraging results showing that short periods of grazing exclusion throughout the year can positively affect plant species composition and productivity, leading to the restoration of long-term overgrazed sites.

As mentioned above, most of the remnants of *Campos Sulinos* grasslands are located on private properties and subject to grazing. In protected areas, the general policy is to remove livestock from their boundaries. Until now, grazing animals have not been used exclusively for conservation management purposes, despite the clear evidence of the benefits of grazing in other regions of the world (e.g., Tallowin et al. 2005; Tälle et al. 2016) and in *Campos Sulinos* grasslands (Baggio et al. 2021), especially at intermediate or low stocking rates (Boavista et al. 2019; Ferreira et al. 2020). In addition to its positive effect on biological communities, incorporating grazing into conservation initiatives is also interesting because it allows the integration of efforts by landowners and stakeholders toward the conservation of biodiversity, which is fundamental for the long-term sustainability of local resources.

Complete exclusion from grazing for extended periods of time leads to a decrease in overall plant community diversity. This exclusion favors a few tall grasses (e.g., *Sorghastrum* spp., *Saccharum* spp.) and shrubs (e.g., *Baccharis* spp., *Vernonanthura* spp.), while negatively impacting species-rich groups that are less effective in competing for light (Overbeck et al. 2005; Ferreira et al. 2020), such as geophytes (e.g., *Oxalis* spp. and *Herbertia* spp.), herbaceous forbs (e.g., *Facelis retusa*, *Wahlenbergia* *linarioides*), prostrates (including grasses like *Axonopus affinis* and herbs like *Hydrocotyle* spp.), rosettes (such as several Asteraceae species like *Chaptalia* spp., *Hypochaeris* spp., *Conyza primulifolia*), and annual plants (e.g., *Vulpia australis*). If exclusion persists over a prolonged period of time, it can result in shrub or wood encroachment (Sühs et al. 2020), gradually replacing species-rich grasslands with a few shrub or tree species.

8.3.2 Grazing by Wild Fauna

Current wild animals in the *Campos Sulinos* are not as large as the extinct Pleistocene fauna, nor as large as animals living in grassland ecosystems in other continents such as North America or South Africa. The region has experienced intermediate levels of defaunation over the last hundreds of years (Bogoni et al. 2020). The largest current herbivores in *Campos Sulinos* include Pampa deer (*Ozotoceros bezoarticus*), marsh deer (*Blastocerus dichotomus*), brown brocket (*Mazama gouazoubira*; Fig. 8.4**c**), greater rhea (*Rhea americana*; Fig. 8.4**f**), and capybara (*Hydrochoerus hydrochaeris*). Capybaras can form large populations and inhabit a wide variety of habitats, including forests, shrubby and herbaceous swamps, wet grasslands, and sandy grasslands, always in proximity with water (Tomazzoni et al. 2005). Greater rheas prefer open areas with vegetation lower than 50 cm and primarily consume wild dicots (Sales 2006). The marsh deer is an endangered species with only three small populations known in the *Campos Sulinos* region (González et al. 2010). Unlike the smaller Pampa deer, the marsh deer feeds mostly on aquatic plants. A study conducted in Argentina, indicates that the presence of cattle and the use of fire can alter the behavior of herbivorous mammals such as capybara, gray brocket, and march deer, potentially leading to more nocturnal behavior (Di Bitetti et al. 2020). There is a lack of studies evaluating the diet and food preferences of these animals specifically in the *Campos Sulinos* region. Studies from neighboring Argentina and other vegetation types suggest that these animals are mixed feeders, consuming both grasses and dicot plants (Jackson and Giulietti 1988; Sales 2006; Desbiez et al. 2011). The impacts of these species on vegetation dynamics are largely unclear; their role today is much smaller than that of domestic grazers, but they could potentially play some management role in protected areas, albeit on a local scale.

In addition to grazing and trampling, other wildlife species may contribute to small-scale patchiness by disturbing the soil and the vegetation through nest-building activities, both above and below the soil level. Animals such as armadillos, burrowing owls, boars, and rodents dig burrows, which can lead to local increases in nutrient availability and burial of surrounding plants (Fig. 8.4**e–f**; Galiano et al. 2014). Ants and mites are considered ecosystem engineers as they cut and process fresh plant parts (e.g., leaves, flowers, fruits) and build nest and galleries, which can indirectly have a positive impact on soil porosity, nutrient enrichment, and decomposition processes (Folgarait 1998; Del Toro et al. 2012). However, the effects of these disturbances are usually localized, allowing for the establishment of more ruderal plants at the disturbed points. In some cases, such as with subterraneous *tuco-tuco* rodents of the genus *Ctenomys*, considerable areas can be affected. Although there have been more studies on the effects of the fauna on vegetation in recent years (e.g., *tuco-tucos*; Galiano et al. 2014 or leaf-cutting ants; Giesel et al. 2020), overall, the effects of fauna on vegetation have been less studied than responses of fauna to grassland management or land use change (e.g., Fontana et al. 2016; Staude et al. 2018; Ferreira et al. 2020).

8.3.3 Fire

In the South Brazilian highland grasslands, fire has been a decisive force in the forest-grassland dynamics and plays a crucial role in maintaining sharp local borders between forest and grassland (Overbeck et al. 2007; Müller et al. 2023, Chap. 16, this volume). Although we have limited data on natural fire regimes, it can be assumed that past burns were triggered by natural events, such as lightning, or set intentionally by indigenous people for activities like hunting. However, in recent times, fires have primarily been ignited by human activities, specifically by farmers who use fire as a management practice to renew pastures for the growing season (Pivello et al. 2021; Paruelo et al. 2022). These controlled fires, known locally as "*sapecadas*," are mild and typically set at the end of winter (Buffon et al. 2018). In the Pampa region, where grazing intensity is in general higher than in the highland grasslands, burning is rarely employed by ranchers due to the lower accumulation of plant biomass (Pivello et al. 2021). However, prolonged droughts can cause fires to spread, as observed during the January 2022 drought, which resulted in over 28,000 ha of burnt area in the Pampa (MapBiomas 2023). In protected areas, fire has recently been used as a management tool, such as in Aparados da Serra National Park. However, the use of fire for conservation purposes remains controversial (Pillar and Vélez 2010), despite evidence of its historical role in these ecosystems. A unique case is the region of granitic hills in the city of Porto Alegre, capital of Rio Grande do Sul state, where the extremely species-rich grasslands undergo burning, usually in the hot summer, primarily initiated by the local population. Since the grassland in this area is ungrazed, the regular fire regime prevents shrub encroachment and forest expansion (Blanco et al. 2014). Although this situation is not typical for the region, where grasslands are usually grazed, the proximity to universities and research institutes has resulted in numerous studies that investigated vegetation dynamics under the influence of these fires, considering both grassland and forest-grassland interfaces (e.g., Overbeck et al. 2005; Müller et al. 2007; see also Müller et al. 2023, Chap. 16, this volume).

Several studies have reported positive effects of fire on the plant community in the *Campos Sulinos*. Fire immediately increases plant species richness, diversity, and evenness (Overbeck et al. 2005). Functional alpha and beta diversities also increase after burning, along with the cover of forbs (Joner et al. 2021). Additionally, fire accelerates certain ecosystem processes, such as litter decay, by exposing the ground to direct sunlight, which enhances photodegradation (Podgaiski et al. 2014). Fire also promotes short-term nutrient availability through the input of ashes into the soil. However, as grassland fires are typically low-intensity fires, their effects are temporary, and approximately 12 months after a fire, plant community and ecosystems processes return to their pre-fire stages (Overbeck et al. 2005). The ability of the *Campos Sulinos* grasslands to recover within one year after burning and restore pre-disturbance levels of diversity and ecosystem processes suggests that the plant community has informational legacy to cope with fire. Many plants have developed characteristics that confer resistance or dormancy to escape from fire (Pausas 2019). The fire resistance strategy involves having thick barks, or dense structures that retain moisture, preventing complete burning of the plants (Pausas 2019). For example, tussock grasses protect their gems with closely packed tillers, forming a dense, more-or-less round structure of green and dry leaves that accumulate humidity and protect internal buds from burning. In grasslands with regular fires, these tussock species (such as *Andropogon lateralis*, *Trachypogon spicatus*, *Sorghastrum pelitum,* or *Aristida* sp.) can become dominant (Overbeck et al. 2005). Rapid bud activation or germination from seeds after fire events is considered dormancy strategies (Pausas 2019). Geophytes that resprout from buds, such as *Sisyrinchium* spp. and *Oxalis* spp., are common in *Campos Sulinos* grasslands, although they do not represent a large portion of the biomass. Seeds from *Andropogon lateralis*, *Chascholytrum subaristatum*, *Schizachyrium microstachyum,* and *Eryngium horridum*, which are all abundant species in the *Campos Sulinos*, are capable of germinating after exposure to 110 °C heat (Overbeck et al. 2006). Notably, fire-triggered seed germination is less common in *Campos Sulinos* compared to the flora of the tropical Cerrado savannas (Overbeck et al. 2006; Silveira and Overbeck 2013).

Given the widespread use of fire in the highland region, particularly in the context of grazing systems, the lack of studies on its effects is surprising, especially considering its potential impact on productivity in grazed grasslands. More studies seem important, both from a basic and an applied research perspective. Basic research is needed, for example, to understand the effect of fire season on vegetation. Currently, fire is usually applied at the end of Southern Hemisphere winter to stimulate resprouting and promote biomass growth for cattle during a period of low fodder availability. Since the *Campos Sulinos* grass flora is a combination of C3/C4 species, different outcomes can be expected from burning in different seasons (Fidelis et al. 2022). For instance, winter burns could have negative effects, especially on the C3 grasses that are physiologically active during this period, but also constitute an important part of forage mass for cattle when the more voluminous C4 grasses are still in a latent phase.

8.4 The Subtle Boundary Between Disturbance and Degradation

Inadequate frequency or intensity of disturbance, whether below or above the optimum level, can lead to degradation: the complete absence of grazing and fire leads to biodiversity losses, while too high grazing intensity leads to overgrazing which also results in biodiversity losses and a decrease in productivity. Finding the balance between disturbance levels that maximize animal production while still maintaining grassland biodiversity and services is a challenge for land managers throughout the *Campos Sulinos* (Andrade et al. 2015). The response to disturbance at the community level depends on community attributes such as resistance (the ability to withstand disturbance) and resilience (the ability to recover after being impacted by disturbance), which are ultimately driven by plant functional diversity and redundancy (Pillar et al. 2013; Joner et al. 2021). The more resistant the plant community is, the better it can maintain regular levels of a given function and service, even under persistent low-intensity or intermittent high-intensity disturbance (Nimmo et al. 2015). Grazing and fire at intermediate levels of frequency and intensity prevent a single or a few species from dominating the community, ensuring the coexistence of species that perform different functions in the ecosystem (Coppedge et al. 2008). Resistance and resilience are the basis of a community's stability (Harrison 1979). When community stability is compromised, changes in the regulation of ecological processes can be expected, subsequently leading to changes in the provision of ecosystem services (Díaz et al. 2018).

Drastic changes in plant community composition can be observed under severe changes in management, such as the total exclusion of grazing (Ferreira et al. 2020). In the *Campos Sulinos*, a highly productive region with high precipitation levels, a change in plant composition can occur within a short period of time (1–2 years; Ferreira et al. 2020), resulting in severe impacts on the stability of ecosystem functions and the provision of ecosystem services. The dominance of woody plants and trade-offs among ecosystem services in relation to management practices can also be observed in the medium term. Therefore, adjusting disturbance to the local characteristics is key for the conservation of grasslands (see also Overbeck et al. 2023, Chap. 17, this volume).

Grazing management has also been identified as part of the solution when exploring adaptations to climate change (Lal et al. 2011). In southern Brazil, severe droughts and reduced productivity in grasslands have been observed in recent years. Additionally, the number of fire events and the affected area have increased. Future research should focus on the potential effects of these processes on plant communities and ecosystems. Areas excluded from disturbance or subjected to low levels of disturbance, where dead plant biomass (grass and shrubs) can accumulate, may become susceptible to wildfires in the *Campos Sulinos*, as seen in the Cerrado and Pantanal ecosystems (Pivello et al. 2021). Research on disturbance and its role in maintaining the biodiversity of grassland ecosystems is essential to ensure the maintenance of biodiversity and quantify its importance for human well-being. Inspired by the enormous complexity of biotic and abiotic relationships in this fascinating ecosystem, science can provide innovative solutions that support diverse plant communities (taxonomic and functional) to be productive and deliver economic prosperity without losing function.

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Chapter 9
Plant Microevolutionary Processes in the *Campos Sulinos*: Why Do They Matter?

Caroline Turchetto, Ana Lúcia A. Segatto, and Loreta B. Freitas

9.1 Introduction

Regionally known as *Campos Sulinos* (Overbeck et al. 2007), the South Brazilian grasslands (Fig. 9.1) include grassy vegetation in the three southern Brazilian states, Rio Grande do Sul (RS), Santa Catarina (SC) e Paraná (PR). The *Campos Sulinos* comprise three main regions, namely the Pampa grasslands in the southern part (Pampa biome, IBGE 2019), South Brazilian Highland Grasslands (SHG) part of the Brazilian Atlantic Forest in RS, SC, and PR (BAF, IBGE 2019), and the *Campos Gerais* in a transitional zone with *Cerrado* (savanna) vegetation in PR (Overbeck et al. 2022). Plant community data support the subdivision of *Campos Sulinos* into two main phytogeographical units, according to IBGE (2019), the lowland Pampa and the Highland Grasslands in BAF (Andrade et al. 2019). These central phytogeographical units agree with the biogeographical division of the region: Pampean, Paraná Forest, and Araucaria Forest provinces (Cabrera and Willink 1980; Morrone

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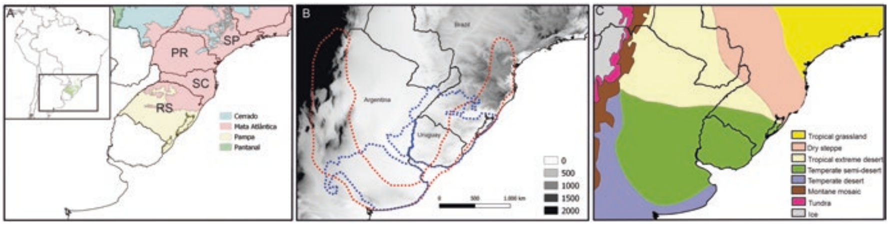

Fig. 9.1 Location of the South Brazilian grasslands (*Campos Sulinos*) in Southern South America. (**a**) Situation of the Pampa region in Rio Grande do Sul Brazilian state (RS), the Brazilian Atlantic Forest (BAF), which includes the South Brazilian Highland Grasslands (SHG), in RS, Santa Catarina (SC), and Paraná (PR), and the SHG-Cerrado transition in PR where we find the *Campos Gerais*; (**b**) The blue dotted line indicates the delimitation of Pastizales del Río de la Plata (based on Soriano et al. 1992) and the red line the Peripampasic Orogenic Arc (based on Frenguelli 1950); (**c**) Vegetation predicted to have occurred in the region during the Last Glacial Maximum (25,000–15,000 years before the present), based on Ray and Adams (2001)

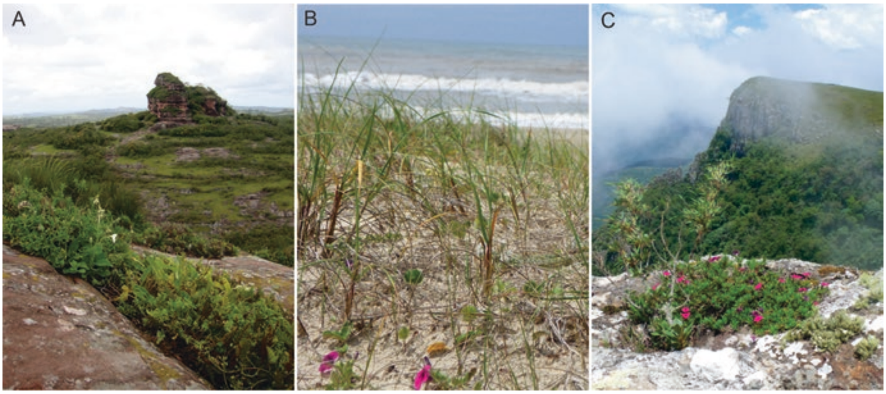

Fig. 9.2 *Campus Sulinos* landscapes. (**a**) *Petunia axillaris* subsp. *axillaris* from the Serra do Sudeste in the Pampa; (**b**) *Petunia integrifolia* subsp. *depauperata* from the South Atlantic coastal plain in the Pampa; (**c**) *Calibrachoa* sp. from South Highland Grasslands. (Photos by: C. Turchetto (**a**), L.B. Freitas (**b**), and G. Mäder (**c**))

et al. 2022). Andrade et al. (2019) described three major vegetation groups in *Campos Sulinos* (highland grasslands, mesic Pampa, and humid Pampa) and identified the particularities of the coastal vegetation, inserted in the Pampa (Fig. 9.2). A refined classification for the highland and mesic and humid Pampa resulted in the proposition of ten grassland groups, demonstrating the heterogeneity of these landscapes where many biotic and abiotic factors drive – or drove in the past – plant diversity. The *Campos Sulinos* division in lowland (Pampa) and highland (SHG) grasslands has also been observed in phylogenetic studies of plant genera that have diversified in this region (e.g., Fregonezi et al. 2013; Iganci et al. 2013; Acosta et al. 2016; Mäder et al. 2019). In this context, it is essential to understand the processes driving the diversification of intraspecific lineages and the origin of new species to interpret and conserve the levels of biodiversity found in the *Campos Sulinos*.

Incrusted into the BAF, the SHG (see Fig. 9.1b) occupy high elevations (> 700 m above sea level). In the northeast of RS and southeast of SC, these grasslands are regionally known as *Campos de Cima da Serra* (Overbeck et al. 2007, Iganci et al. 2011). Mosaics between grassland and forest with the dominant arboreal species *Araucaria angustifolia* (Bertol.) Kuntze are the typical primary vegetation in these areas (Iganci et al. 2011, Andrade et al. 2019). The SHG was the stage for several processes of plant diversification and speciation and currently houses many endemic species (Iganci et al. 2011). Floristic studies have revealed high similarity between the SHG and Andean floras, reflecting past connections between these areas (Safford 2007, Antonelli 2022). In the southern portion, in the transition between BAF and Pampa (~29° and 30°S), a region known as 'Portal de Torres' (Rambo 1950), there is a biogeographical break that has been associated with marked differentiation between northern and southern populations for some plant species (Pinheiro et al. 2011, Turchetto-Zolet et al. 2016). It is worth mentioning that this pattern was found in plants that do not grow in grassland formations in BAF, occurring most in coastal areas that are also included in the Pampa.

The Pampa region is an open and mainly flat region, with elevations not above 500 m above sea level, dominated by grassy formation where the vegetation is predominantly herbaceous. The area extends from the southernmost RS and the entire Uruguayan territory to the Pampa province in central-eastern Argentina (Morrone 2014; Morrone et al. 2022), forming a region collectively known as Río de la Plata grasslands (Soriano et al. 1992) (Fig. 9.1). In the Pampa, forest components are scarce, found mainly along river banks and in areas with irregular geographical reliefs such as the Serra do Sudeste (Rambo 1956; Boldrini 1997; Hasenack et al. 2010), constituting a mosaic with elements from the coastal BAF and grasslands on shallow soils (Oliveira- Filho et al. 2015).

The maintenance of the *Campos Sulinos* landscape features has been discussed in terms of historical disturbances, such as grazing by now extinct herbivores (Lopes et al. 2020), the historical practices of livestock management (Boldrini and Eggers 1996; Nabinger et al. 2000; Carvalho et al. 2006; Overbeck et al. 2007; Pillar and Vélez 2010), and the presence of fire, especially in the SHG (Behling et al. 2004). Moreover, other factors have been pointed out as drivers of the absence of arboreal species in the Pampa, such as edaphic and climatic characteristics (Milewski and Mills 2015; Rezende et al. 2018; Segovia et al. 2020). Although anthropogenic disturbing has historically shaped this landscape, overgrazing (Nabinger et al. 2000), and land use for agriculture (Antoneslli 2022) can lead to a significant loss of natural areas and, consequently, to lose under-evaluated plant diversity (Overbeck et al. 2007). However, few studies have attempted to explore the microevolutionary processes (Turchetto-Zolet et al. 2013; Leal et al. 2016) involved in the origin and maintenance of the biodiversity from *Campos Sulinos*.

Several plant groups are widely distributed in the *Campos Sulinos*, such as the two Solanaceae genera *Petunia* Juss. and *Calibrachoa* Cerv. These genera are closely related clades (Särkinen et al. 2013; Reck-Kortmann et al. 2015) that display many morphological, ecological, and evolutionary similarities. Species of *Calibrachoa* and *Petunia* were considered as the same genus until the mid-1980s. Except for *Calibrachoa parviflora* (Juss.) D'Arcy that has a cosmopolite distribution, likely due to accidental dispersal through commercial activities; all taxa are endemic to southern South America, occupying the subtropical grasslands at different elevations. Usually, populations grow in open areas, often in disturbed sites such as road slopes, and are found in small patches of just a few to dozens of plants. In the *Campos Sulinos* region, it is possible to find 12 of the 14 *Petunia* (Stehmann et al. 2009) and 21 of the 27 *Calibrachoa* (Fregonezi et al. 2012) species, many times with species of the two genera growing close to each other at the same place. The genus *Petunia* is divided into two main clades corresponding to the corolla tube length, short and long tube clades. The short tube clade is split into two subclades related to the local elevation where species occur, lowlands and highlands (Reck-Kortmann et al. 2014). The *Calibrachoa* species are distributed in two subgenera. One (*Calibrachoa*) encompasses only two species, whereas the second (*Stimomphis*) groups the remaining species. The subgenus *Stimomphis* revealed four main subclades related to their ecological niche conservatism and species geographical distribution (Mäder and Freitas 2019). Other plant groups occupying the same region show a similar pattern of speciation evolving under the same ecological constraints (Barros et al. 2015), such as the clade *Adesmia* ser. *Psoraleoides* Burkart (Leguminosae). *Adesmia* ser. *Psoraleoides* encompasses 11 species endemic to the *Campos de Cima da Serra* that occupy small patches of grasslands, usually forming populations with few individuals. Results based on molecular markers suggested these species diverged during the Pleistocene, with speciation driven by climate changes, after migrating to the highlands (Iganci et al. 2013).

The evolutionary history of *Petunia* and *Calibrachoa* reported that they originated in the Pampa region, the southernmost limit of their distribution, from which they migrated and diversified (Reck-Kortmann et al. 2014; Mäder and Freitas 2019) under the influence of Pleistocene climate changes (Barros et al. 2015, 2020). Plant-pollinator interactions and local adaptation due to differences in ecological conditions (Fregonezi et al. 2013) were also proposed to drive the diversification of both genera. Microevolutionary processes such as hybridization, gene flow, genetic drift, founder effect, and changes in effective population size have been implicated in species distribution and diversification.

We discuss the microevolutionary processes driving plant diversification in *Campos Sulinos*, mainly using the *Calibrachoa* and *Petunia* genera as models. We will include species that occur outside the *Campos Sulinos* region as defined above, for example, when they inhabit the other parts of the *Pastizales del Río de la Plata* region, e.g., in Uruguay or Argentina. We also will point out knowledge gaps on the topic for the region and discuss the potential to use data on intraspecific genetic diversity to propose conservation efforts.

9.2 Processes Driving the Diversification of Intraspecific Lineages in the *Campos Sulinos*

The historical climate changes during the Quaternary glacial and interglacial cycles played a crucial role in the distribution of plant species in the northern (Hewitt 2000) and southern hemispheres (Behling 2002; Behling et al. 2005). In South America, fully-formed glaciers occurred only in the Andes. In the remaining areas, climate changes promoted contraction and expansion in closed vegetation (forests) and open formations (grasslands) as glacial and interglacial periods alternately succeeded. Such shifts resulted in complex histories regarding the establishment and composition of current vegetation more than simple local extinctions and typical glacial refugia. The climate changes at the Last Glacial Maximum (LGM) and early Holocene (ca. 12,000 years ago) impacted species distribution and diversity, with cold-sensitive species exhibiting a contraction in their distribution. Forest-adapted species migrated in direction of the Equator during the cold and dry periods or became protected in humid and warmer areas such as the gallery forests, according to the Quaternary refugia hypothesis (Haffer 1969; Carnaval et al. 2009).

In turn, cold-adapted species expanded their distribution simultaneously, contracting their range during the interglacial cycles when their distribution was fragmented due to the rapid expansion of forest species and, with this, closed vegetation. Wet and occasionally dry, open habitats, often sandy and salty soils, were prone to provide home to cold-adapted grassland species during the glacial periods, favoring migration and diversification. The warmer and wetter climate that promoted forest growth isolated the newly established populations, possibly leading to allopatric speciation (Behling and Negrelle 2001; Behling 2002; Lorenz-Lemke et al. 2010).

Despite the less severe effect in the Southern Hemisphere, the Quaternary glacial and interglacial cycles appear in many works as drivers of diversification in the *Campos Sulinos* (e.g., Iganci et al. 2013; Mäder et al. 2013; Barros et al. 2015; Moreno et al. 2018) that have resulted in the composition of the current vegetation. Despite advances (e.g., Andrade et al. 2023) species diversity in the region as a whole is still poorly known. Contrary to what was thought until recently, the region is highly diverse in terms of plants and harbors many endemic species (Iganci et al. 2011; Fregonezi et al. 2013; Turchetto-Zolet et al. 2013).

Different factors acting on small geographical scales affected the current plant diversity of *Campos Sulinos*. For example, changes in the sea level during the Pleistocene were responsible for the genetic structure and diversification of plants in the coastal region, the Southern Atlantic Coastal Plain (SACP) that extends from Uruguay to the South of Santa Catarina Brazilian state. Geological and ecological analyses have demonstrated that SACP was formed while marine transgressions and regressions shaped the dune lines during the Quaternary climate changes over the past 400,000 years (Dillenburg and Hesp 2009; Martinho et al. 2010).

The presence of paleochannels, i.e., barriers to genetic exchange caused by marine transgressions, is crucial in explaining the intraspecific genetic structure observed in some plant species occurring in SACP. *Calibrachoa heterophylla*

(Sendtn.) Wijsman (Solanaceae) is a species distributed predominantly in the SACP, occupying dunes and sandy grasslands (Mäder et al. 2013). Based on phylogeographical and demographic analyses, we know that the extant populations are genetically structured, as a result of the paleochannels that limited the species' dispersal. Such historical barriers structured the species' genetic diversity throughout the SACP that currently shows spatial structuring, even though no conspicuous geographical barriers exist in the present. This *Calibrachoa* species, with a typical linear distribution in the coastal region, shows limited and asymmetric gene flow, mainly influenced by geographical distance; evolutionary lineages of the species are currently maintained due to ecological constraints, such as the climate and wind direction and intensity (Silva-Arias et al. 2021).

Marine transgressions/regressions during the late Pleistocene also affected the taxon *Petunia integrifolia* subsp. *depauperata* (Fries) Stehmann and Semir, part of the *P. integrifolia* (Hook.) Schinz & Thell (Solanaceae) species complex (Longo et al. 2014). This taxon diverged from the sister species, *P. integrifolia* subsp. *integrifolia,* near the coast as SACP land area became available for colonization (Ramos-Fregonezi et al. 2015). The taxon is divided into four evolutionary lineages that occupy the sand barriers parallel to the coast. The population genetic analyses indicated the presence of many founder effects as the taxon's ancestor was restricted to refugia during periods of high sea level and recolonized the coast when the sea level regressed (Ramos-Fregonezi et al. 2015). The four evolutionary lineages are locally adapted and with a strong founder effect (Silva-Arias et al. 2017) that is maintained by ecological conditions that diverge along the coastline (Guzmán et al. 2022). A similar phenomenon was reported for populations of *Turnera sidoides* L. (Passifloraceae, Turneroideae; Moreno et al. 2018) and *Petunia axillaris* subsp. *axillaris* (Lam.) Britton et al. (S. Guzmán et al., 2022) found close to the SACP, suggesting a heterogeneous landscape in the past, where transient barriers to gene exchange were present.

Refugia theory and rivers acting as phylogeographical barriers have been suggested to explain the emergence of new evolutionary lineages in species of *Petunia* from the Pampa (Giudicelli et al. 2021) and also among species from the SHG (Soares et al. 2023). Both phylogeographical processes were strongly influenced by climate changes that were responsible for range fragmentation and isolation of populations of the species, limiting gene flow and eventually leading to diversification.

In South American grasslands, the formation of the Peripampasic Orogenic Arc (Frenguelli 1950) has recently been related to the intraspecific genetic diversity distribution in *Turnera sidoides* (Moreno et al. 2018) and *Opuntia bonaerensis* Speg. (Cactaceae) (Köhler et al. 2020). The Peripampasic Orogenic Arc corresponds to a range of mountains that extends from the sub-Andean region in Argentina to Uruguay and southern Brazil and constitutes a continuum for the distribution of several animal species (e.g., Ferretti et al. 2012; Silva et al. 2018). With more accentuated topography, these mountains harbor many endemic species (Crisci et al. 2001; Moreno et al. 2018). The biotic connection among the units in this mountain chain probably ceased during the Tertiary tectonics (Mattoni and Acosta 1997; Crisci et al. 2001). For some grassland-adapted taxa, these higher elevations acted as local refugia during the warmer times in the Pleistocene when the forest expanded. For *Petunia*, the geological formation of the Peripampasic Orogenic Arc in *Serra do Sudeste* region in RS is considered as a diversity center, with at least five taxa being found there (Stehmann et al. 2009). Several *Calibrachoa* species are endemic to the region (Fregonezi et al. 2012). For both genera, the analysis of genetic diversity indicated similar microevolutionary processes acting to shape the population structure.

The expansion of geographical distribution in *Petunia* species throughout the *Campos Sulinos*, and probably among the species of *Calibrachoa*, followed a center-periphery pattern, with morphological and genetic novelties appearing on the borders, many times promoting speciation or originating new intraspecific lineages (Freitas 2022). Lower genetic variability (Silva-Arias et al. 2017, 2021), changes in the reproductive system (Turchetto et al. 2015), and founder effects (Backes et al. 2019; Souza et al., 2022), with genetic drift and isolation by distance as the main factors to explain the population structure are observed in the borders of species range. This entire process occurred under the climate changes that modified the landscape in *Campos Sulinos* (Barros et al. 2015, 2020).

In SHG, grasslands form mosaics with the Araucaria Forest, with the proportion of the two contrasting vegetation types fluctuating over the past millenia due to Quaternary climate variation. The genetic diversity of these species reports the shifts promoted by the climatic cycles on their geographical distribution and population structure. The Quaternary climate cycles would promote the fragmentation of broadly distributed grassland ancestors, isolating populations that, after several generations, diversified and speciated. Many examples described this hypothesis from the view of population genetics. Species of *Petunia* that occupy the SHG form a well-supported clade (Lorenz-Lemke et al. 2010; Reck-Kortmann et al. 2014) with low morphological and genetic divergence. The species divergence occurred in allopatry during the Pleistocene (ca. one million years ago). Each species revealed the strong effect of genetic drift and local adaptation on the establishment and structure of its populations (Souza et al. 2022). As observed in *Petunia*, herbaceous and subshrubs species of *Calibrachoa* that inhabit the SHG showed a similar evolutionary scenario (John et al. 2019). They constitute a well-supported clade (Mäder and Freitas 2019) with low genetic diversity, indicative of a founder effect and expansion and contraction of their geographical range during the Quaternary climate cycles. To the north, occupying the highland grasslands associated with rock outcrops in PR, only *Calibrachoa* species are found, constituting a well-supported clade in the genus' phylogenetic tree. These species display a rapid morphological divergence (Fregonezi et al. 2013) and low levels of genetic differentiation due to their evolutionary proximity (Mäder and Freitas 2019). They share many genetic polymorphisms, and their divergence was related to a rapid speciation process due to the fragmentation of the common ancestor's distribution during the climate changes that isolated the lineages, allowing local adaptation. The populations of *Hypochaeris catharinensis* Cabrera (Asteraceae), a perennial herb endemic to the *Campos Sulinos* of high elevation, show high levels of genetic differentiation with no correlation between geographical and genetic distances. This pattern may be associated with multiple founder events in similar ecological niches (Chaves et al. 2019).

The soil is another important ecological factor that differentiates the grasslands in *Campos Sulinos*. In SHG, the soil is predominantly dry, rocky, and shallow, resulting from basalt weathering. In the Pampa, soils originated from sedimentary substrates predominate, with variation from sandy and shallow (e.g., in the coastal region) to deeper and with more clay. The soil in Peripampasic Orogenic Arc is derived from an igneous plutonic geological substrate and is also shallow (Santos et al. 2011; Andrade et al. 2019). Such heterogeneity led several authors to propose the division of the Pampa into smaller provinces or regions (Overbeck et al. 2007) according to soil structure, origin, and composition. Some phylogeographical studies conducted for plant species from these areas (e.g., Fregonezi et al. 2013; Turchetto et al. 2014a, b; Silva-Arias et al. 2017) proposed abiotic factors as drivers for intraspecific lineages diversification or speciation. In species with a distribution that crosses the limits of *Campos Sulinos*, such as *Petunia axillaris* subsp. *parodii* Steere (Giudicelli et al. 2021), adaptation to different soil types and climatic variables may partly explain the observed genetic diversity.

Besides historical climate changes and soil types, contemporary climatic differences throughout the *Campos Sulinos* maintained the evolutionary lineages of different species (e.g., Silva-Arias et al. 2017, 2021; Barros et al. 2020). For *Petunia* and *Calibrachoa* species, characteristics of the precipitation regime constrained the intraspecific molecular diversification without changing the speciation rates. The precipitation seasonality strongly influenced genetic structure, possibly reflecting the recent maintenance of species boundaries (Barros et al. 2020). On the other hand, there are species whose lineages showed no structured populations despite occurring in sites with different microclimates and soils and that also evolved under the Pleistocene climate changes. For example, *Tillandsia aeranthos* (Loisel.) LBSm. LC (Bromeliaceae), which has high gene flow and high levels of genetic diversity among populations, is found in dense populations, predominantly in riparian forests in the Pampa grasslands and marginally in the BAF and Chaco ecoregions. Demographic analyses conducted with this species indicated stability and probably no effect of Late Quaternary climatic cycles (Aoki-Gonçalves et al. 2020). This could be related to the establishment of refugia in riparian forests (Meave et al. 1991; Kellman et al. 1996) or to the species' habit (epiphytic) and reproductive system (frequently clonal).

A general evolutionary scenario indicates that the current distribution of species and intraspecific lineages is an intricate and complex net between historical and contemporary processes and species-specific characteristics. Therefore, more studies are necessary to fully understand the diversification processes in *Campos Sulinos* and protect all the different lineages. Future studies should represent the phylogenetic diversity of plants from the *Campos Sulinos*, as most microevolutionary studies conducted so far focused on only a few plant families and genera. In addition, studies on species displaying different reproductive characteristics, such as pollination mode and seed dispersal, and different geographical distribution patterns (narrow vs. widespread) in the *Campos Sulinos* would be crucial to understand the microevolutionary process involved in plant lineage diversification.

9.3 Biotic and Abiotic Factors Influencing Plant Adaptations in the *Campos Sulinos*

Human colonization in southern Brazil coincides with a warmer climate in the Holocene, which increased the presence of fire. During the last 4000 years, the weather became more humid, allowing the expansion of forests (Ledru et al. 2005). Cattle and horses were introduced in the region by European settlers in the seventeenth Century. Since then, human interference has played a vital role in the maintenance of *Campos Sulinos*, preventing forest expansion over grassland (Overbeck et al. 2007). However, the dynamic between anthropogenic preservation and disturbance in *Campos Sulinos* is still poorly understood, which increases the risk for the biodiversity in the region (Pillar and Vélez 2010; Overbeck et al. 2018). More recently, monocultures of *Eucalyptus* L'Hér. and *Pinus* L. species are spreading throughout the *Campos Sulinos*, threatening native species also due to uncontrolled invasion of their habitats.

Moreover, soybean, wheat, rice and other crops occupy a significant portion of the Pampa, reducing natural habitat, displacing the native species and also affecting remnant ecosystems. For example, in regions with stronger conversion rates, losses of plant and animal diversity occurred in remaining grasslands (Staude et al. 2017), with impacts also on ecological interactions. Plant-pollinator relationships are an essential biotic factor in ensuring the structure of communities (Wolowski et al. 2017). These interactions in *Campos Sulinos* are diverse and reflect the heterogeneity of the habitat. Bees are the most frequent pollinators, and many plant species are visited by more than one group of pollinators (Oleques et al. 2020). For example, *Petunia* species display flowers that vary in shape, color, and aroma emission and composition, attracting different groups of functional pollinators, such as bees, hawkmoths, and hummingbirds. These species offer rewards such as pollen and nectar and have a close relationship with their pollinators (e.g., Wittmann et al. 1990; Rodrigues et al. 2018). At least one group of these plant species evolved under pollination syndrome pressure (Fregonezi et al. 2013; Reck-Kortmann et al. 2014; Segatto et al. 2016). Despite some hybridization events (Turchetto et al. 2014a, b), the *Petunia* species with long corolla tubes keep the boundaries between them due to microenvironmental adaptation (Caballero-Villalobos et al. 2021) and some changes in their reproductive system (e.g., Turchetto et al. 2015). In the face of hybridization, morphological and genetic novelties appear (Teixeira et al. 2020) and, with stable hybrid populations (Schnitzler et al. 2020), hybridization increases the intraspecific diversity and generates new evolutionary lineages (Turchetto et al. 2019b).

Each *Petunia* species in the long corolla tube clade has a different floral syndrome, and their flowers reflect specialization to a different pollinators' group (Hoballah et al. 2007; Venail et al. 2010; Hermann and Kuhlemeier 2011; Klahre et al. 2011; Sheehan et al. 2012, 2016; Hermann et al. 2015; Berardi et al. 2021). The white-flowered *Petunia axillaris* (Lam.) Britton, Sterns & Poggenb. displays traits associated with pollination by hawkmoths. The bright-red flowers of *P. exserta*

Stehmann show all the attractive features for hummingbirds (Lorenz-Lemke et al. 2006). The pink-flowered *P. secreta* Stehmann & Semir has floral traits usually observed in bee-pollinated species. These three species co-occur in the *Serra do Sudeste* (part of the Peripampasic Orogenic Arc), although each species inhabits different microenvironments (Segatto et al. 2014; Turchetto et al. 2014a, b, 2022; Rodrigues et al. 2018).

Hybrids between *P. axillaris* and *P. exserta* can be frequently found in nature, and, despite not being formally studied, hummingbirds have been observed visiting both species, which suggests that these birds may act as vectors for hybridization (Lorenz-Lemke et al. 2006; Segatto et al. 2014; Turchetto et al. 2019a, b). However, the viability of hybrids is probably limited by postzygotic isolation (Caballero-Villalobos et al. 2021; Turchetto et al. 2022). At least in these closely related *Petunia* species, the floral isolation is not complete. Turchetto et al. (2015, 2022) estimated the gene flow for each species and revealed that most parentals are from the same population, independently of the spatial distance between patches of individuals. Indeed, *P. axillaris* became self-compatible in this area. All hybrid individuals are found in the same environment as *P. exserta,* sharing with this parental several potentially under-selection markers (Caballero-Villalobos et al. 2021). Despite differences in floral morphology in each species (Teixeira et al. 2020) that attract different pollinators, these species form stable hybrid populations (Schnitzler et al. 2020), keeping their limits (Turchetto et al. 2019a, b). The interaction between floral syndromes and abiotic factors may have shaped the observed diversity, exemplifying the importance of integrative studies to elucidate microevolutionary processes (Segatto et al. 2017).

Studies that evaluated the pollen flow between populations of the species *P. secreta* (Rodrigues et al. 2019), *P. axillaris* (Turchetto et al. 2015), and *P.* exserta (Turchetto et al. 2022) indicated high levels of self-fertilization, especially in populations that are found spatially close to others. The self-fertilization in these cases could maintain the species boundaries even in the face of sporadic interspecific hybridization events. Based on the phylogenetic character reconstruction, the ancestral of these closely related *Petunia* species was self-incompatible (Reck-Kortmann et al. 2014). Indeed, controlled crosses (Robertson et al. 2011) indicated that most *Petunia* species are self-incompatible and follow the Solanaceae self-incompatibility type (Williams et al. 2015). *Petunia axillaris* subsp. *axillaris*, *P. secreta,* and *P. exserta* are closely related species (Reck-Kortmann et al. 2014), and the occurrence in a rock formation in the *Serra do Sudeste* region represents the north edge of the distribution of the widespread *P. axillaris* subsp. *axillaris* (Turchetto et al. 2014a, b). The transition in the reproductive system of these species could reflect the colonization of a new environment as the three species grow in a peculiar landscape in the *Serra do Sudeste*, as proposed in Baker's Law, with the establishment of a new population in an unoccupied habitat, often by a small number of individuals able to reproduce (Pannell 2015). The sandstone towers in the Guaritas region are distinct from the preferential habitat for the other *Petunia* species (Stehmann et al. 2009). The self-compatible status of these lineages could have been fundamental during the colonization process, for example, for *P. axillaris* subsp. *axillaris* that has self-compatible and self-incompatible populations throughout its geographical range (Ando 1996; Gleiser et al. 2014; Turchetto et al. 2015).

Few studies evaluated the intraspecific genetic lineages and adaptation to environmental conditions in *Campos Sulinos*. Some of these works have used potentially under selection (outlier loci) genomic SNPs to investigate the association with soil and current climatic conditions on the geographical distribution of intraspecific genetic lineages (Giudicelli et al. 2021; Guzmán et al. 2022; Pezzi et al. 2022). Giudicelli et al. (2021) studied one subspecies of *P. axillaris* occurring in Pampa grasslands in RS and Uruguay. They found that the drivers of genetic differentiation between populations based on the outlier loci were most related to the climatic variables. In contrast, based on the neutral loci geographical distance, mainly the isolation by distance model, better explained the diversity between population groups. In this study, genetic drift and selection also could be involved in the patterns of intraspecific genetic diversity and divergence in this taxon.

On the other hand, Guzmán et al. (2022), using extensive genomic coverage, suggested that neutral and selective forces equally promoted diverging genetic distribution in a *Petunia* species complex distributed in Pampa from SACP to inland. This study found that drivers of genetic divergence between two genetic lineages related to the SACP and inland regions were primarily associated with geographical distance and humidity based on outlier loci and geographical distance and atmospheric radiation according to neutral loci. This study showed the connection between adaptation and environmental heterogeneity found in the Pampa region as a driver for the origin of evolutionary lineages.

Pezzi et al. (2022) analyzed another *Petunia* species complex occurring in a transitional zone between Pampa grasslands and BAF based on genomic data. They found that species diverged during the Pleistocene climate changes and probably came into secondary contact during Holocene, leading to limited gene flow between them. Climatic variables and altitude mainly explained the genetic divergence between lineages. *Petunia* and *Calibrachoa* are good examples of the microevolutionary processes in the *Campos Sulinos* and can serve as models for studying local adaptation to biotic and abiotic factors. More works, including other species and genomic datasets, would improve the knowledge of abiotic factors driving genetic diversity.

Ecological processes and environmental forces shaped the vegetation on Earth (Rull 2011), and climatic factors played a crucial role in species diversification because they can modify the landscape. Selection mediated by ecologically divergent forces promotes lineage differentiation, and distinct lineages can experience shifts to different directions in changing environments. Thus, isolation by distance (allopatric speciation), isolation by environment (local adaptation), and isolation by colonization (center-periphery distribution) are implicated in the origin of diversity. *Petunia* and *Calibrachoa* are good examples of the microevolutionary processes carried out in the *Campos Sulinos* under climate changes.

9.4 Microevolutionary Processes and Evolutionary Potential Facing Anthropogenic Impacts

Human actions immediately impact the natural environment, and we live in a moment of crisis with climate changes and intense biodiversity loss. Genetic diversity is one of the three main pillars of biodiversity. Essentially, it is the substrate for evolution, as biological evolution changes the allele frequency in a population over time (Wilson and Bossert 1971). The loss of evolutionary potential could hinder species' ability to adapt to changes. Quantifying the differentiation patterns is essential to understand processes such as local adaptation and incipient speciation, which are critical information for conservation genetics (Gambra and Muchlala 2020) and provide fundamental tools to guide conservation and restoration (Krammer and Havens 2009; Aavik and Aveliina 2018). Estimating the intraspecific genetic diversity allows the evaluation of the genetic risks associated with a particular species, such as changes in population size, degree of isolation, and fitness, thus suggesting potential management strategies (Ellstrand and Elam 1993). Moreover, the intensity and distance of gene flow in plants can be used to determine the actual evolutionary units (Ellstrand 2014) and estimate invasiveness evolution (Schierenbeck and Ellstrand 2009).

Global warming affects temperature that influences the rain regime. Water unavailability is an essential component of climatic stress (Konapala et al. 2020). However, the drought stress due to either low precipitation (relative to evapotranspiration) or precipitation seasonality may have also shaped the distribution of plant diversity (Neves et al. 2020), which was demonstrated for plant species from the SHG (Barros et al. 2015). A recent study has suggested that the expansion of arid environments likely led to evolutionary diversity loss (Neves et al. 2021). One tool that has been used to predict how climate changes impact the species' ranges (Kane et al. 2017; Backes et al. 2019; Giudicelli et al. 2019) is identifying suitable areas for species occurrence in the future. Including intraspecific genetic data allows for estimating the species' distribution under climate changes more accurately than using only occurrence data (Rolland et al. 2015; Razgour et al. 2019). The higher accuracy is due to the population processes, and intraspecific variability is fundamental for species to keep their distribution and adapt to changing environments (Bellard et al. 2012; Hu et al. 2021).

Evolution within species and populations can occur rapidly in response to human actions, which would be especially tense for endemic species (Manes et al. 2021). To date, there are no previous studies including the intraspecific genetic information to predict the impacts of future climate changes on plants distributed throughout the *Campos Sulinos*. L. Caballero-Villalobos et al. (unpublished data) have forecasted the potential effects of ongoing climate changes on the range, genetic diversity, and population structure for eight *Petunia* and *Calibrachoa* species with different distribution ranges in SGH and Pampa. For species narrowly distributed in SGH and *Serra do Sudeste*, the results are scary, with the decrease or total loss of genetic diversity and evolutionary units for most taxa, even under the most optimistic scenario (IPCC 2023 available at https://www.ipcc.ch/). For the species occurring in SACP (*Calibrachoa heterophylla* and *Petunia integrifolia* subsp. *depauperata*), on the other hand, a fragmented suitable area has been predicted, identifying potential future refugia for species persistence. This study highlights the importance of preserving the intraspecific genetic diversity found in these species, holding their potential to adapt to environmental changes and the found genetic lineages. The loss of potential distribution in the face of future climate changes also was observed in an indicator tree species from the *Araucaria* Forest (Saraiva et al. 2021). However, the current protected areas are not efficient enough to cover climatically suitable areas for this arboreal species throughout its distribution.

Moreover, as previously mentioned, the evolutionary history of SGH is closely related to grassland-forest dynamics during past climatic fluctuations (Behling 2002; Behling et al. 2005), especially regarding the *Araucaria* Forest. This location has been considered as refugia in the southern BAF during the past 30 Kya (Costa et al. 2017), with species presenting high genetic diversity (Raposo do Amaral et al. 2013; Barros et al. 2020). These studies highlight the importance of conserving these natural habitats.

Several studies suggest that prudent conservation strategies must incorporate potential differences in climate tolerance among lineages when planning conservation measures in the face of environmental changes (e.g., D'Amen et al. 2013; Paz-Vinas et al. 2018; Coates et al. 2018; Quiroga et al. 2019). A recent study highlighted the importance of considering intraspecific genetic data to biodiversity conservation post-2020 and showed a schematic strategy to incorporate genetic data to monitor biodiversity (Hoban et al. 2021). Considering three microendemic *Petunia* species, similar suggestions were proposed to preserve grassland species from SHG (Souza et al. 2022).

The population structure of widespread species can reflect different evolutionary processes, such as local adaptation. The widespread *Petunia axillaris* is a good example, occurring in the Pampa and adjacent grassland formations; this species has distinct evolutionary lineages emerging with the past climatic oscillation during the Pleistocene (Turchetto et al. 2014a, b; Giudicelli et al. 2019). Within the Pampa region, these lineages occur in the East-West direction in RS and Uruguayan territories. They have different effective population sizes and demographic responses over time (Turchetto et al. 2014a, b; Giudicelli et al. 2021) regarding the changes in suitability of the climatic area for the different lineages (Giudicelli et al. 2019). The potential response to future climate changes for the different lineages predicted individual responses, with the expansion of the population located in the West and fragmentation for the eastern-located populations. Considering this scenario, estimating the levels of gene flow between populations of each lineage is essential to identify the amount and distribution of genetic diversity. The populations of this species are firmly structured in the eastern lineage (Giudicelli et al. 2021), and the genetic structure could be determined due to genetic drift and selection. In this case, it could be better to preserve diversity establishing multiple small areas of protection than one larger area.

Estimating population structure is also vital to track the success of invasive species. Humans disrupt many natural processes for alien species that determine genetic diversity (founder effect, genetic drift, gene flow, natural selection), mainly because of repeated introduction sources that restore genetic bottleneck and long-distance dispersal and allow the gene flow between different genetic origins. These actions can increase genetic diversity in these plants, making them aggressive competitors to native species (Le Roux et al. 2006; Smith et al. 2020). This can be the case of *Senecio madagascariensis* Poir. (Asteraceae), native from southern Africa and accidentally introduced in Australia (Dormontt et al. 2014), the Hawaiian Islands (Le Roux et al. 2006), Argentina (López et al. 2008), and Brazil (Matzenbacher and Schneider 2008), where it has spread quickly throughout the Pampa (Mäder et al. 2016). In the Pampa, *S. madagascariensis* was introduced multiple times, which could have increased the genetic diversity and the potential to species establish and persist a long time.

9.5 Conclusions, Gaps, and Perspectives

The human influence on South American biodiversity has led many plant species to disappear quickly. This loss will potentially impact ecosystem services, climate, and people (Antonelli 2022 and is particularly critical for the *Campos Sulinos* region, which has experienced rapid and extensive impacts from human activities, such as land use for agricultural practices and grazing. The *Campos Sulinos* has a high diversity, not yet totally known (Overbeck et al. 2007; Leal et al. 2016).

It is necessary to incorporate evolutionary thinking into decision-making to preserve and restore endangered areas and species, describing, monitoring, and basing action on genetic diversity estimates (Hoban et al. 2021). This chapter pointed out important knowledge gaps in the plant microevolutionary processes and explored some perspectives to improve the use of population genetic data to conserve and restore the *Campos Sulinos* (Fig. 9.3).

We discussed some results of population genetic studies, mainly focused on a particular group of plants for which such information is available. For example, taking the consequences of the geographical distribution of the intraspecific lineages of a widespread species in the Pampa (Turchetto et al. 2014a, b; Giudicelli et al. 2021), we observed that the microevolutionary process might follow the divisions of the Pampa in different phytogeographical regions (Boldrini 1997; Hasenack et al. 2010). The diverse landscapes in Pampa are related to differences in soil and plant composition, especially regarding more representative botanical families in the region, such as Poaceae and Fabaceae (Boldrini et al. 2010). Therefore, it is necessary to conduct more studies considering intraspecific genetic diversity with plants from this region (Turchetto-Zolet et al. 2013; Leal et al. 2016) to highlight the role of microevolutionary processes on the biodiversity of the *Campos Sulinos*. Future studies should select indicator species with different distribution patterns, widespread and narrowly distributed, with further land use,

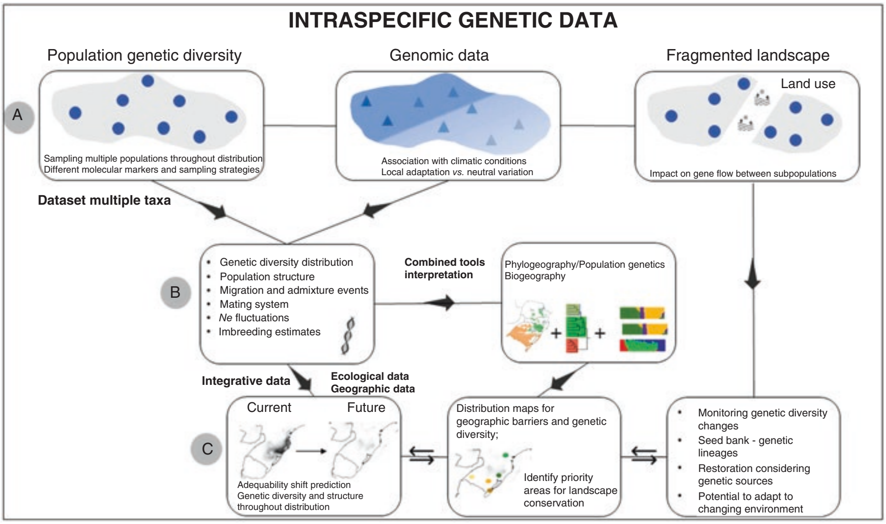

Fig. 9.3 Schematic representation of the steps necessary to study plant microevolutionary processes that can help understand the drivers of evolution and be applied in conservation efforts in the *Campos Sulinos. A) Examples of sampling strategies and datasets. B) Tools of analysis. C) Integrative studies and application of genetic diversity to conservation*

encompassing representative botany families in these landscapes, such as Poaceae, Fabaceae, and Asteraceae.

It is necessary to obtain population genetic data for plant species from the *Campos Sulinos* to reveal the processes impacting genetic diversity and gene flow (the connection between populations on the landscape). Plant population differentiation could be driven by multiple biological processes, such as pollination, seed dispersal, mating, and growth form (Gambra and Muchhala 2020). Thus, genetic studies are crucial to characterize species with different life histories and run integrative studies. These studies reveal a synthesis of patterns and certain particularities in population processes. They get started to apply this information to identify regions with high genetic diversity, estimate gene flow in different systems, and incorporate microevolutionary processes into the current and future ecological modeling (Razgour et al. 2019) for plants and their pollinators and predators (Kort et al. 2018) (see Fig. 9.3 for suggestions on these workflows).

Land-use changes are the main threat to Neotropical plant species (Antonelli 2022). The MapBiomas project (available at https://mapbiomas.org/) recently alerted to the intense loss of natural areas in the *Campos Sulinos* due to agricultural practices, leading to habitat fragmentation for native species. Habitat fragmentation is one of the most damaging risks for species persistence. It limits the dispersal with consequences in population effective size and additional problems such as the edge effect (Murcia 1995). Dispersal on a landscape scale is a crucial process to maintain genetic diversity. In this sense, future studies should use population genetic data to assess the impact of habitat loss and fragmentation on the connectivity and regional survival of wind-dispersed and animal-dispersed plant species. The experimental designs should compare impacted and preserved areas, selecting widespread species to observe the effect of environmental degradation on the genetic diversity and population structure.

Studies that estimate the number of significant evolutionary units (ESUs) help identify priority areas for conservation. The genomic tools can help delineate conservation units when assessing the impacts of global climate changes (Funk et al. 2012) as they incorporate neutral and potentially under-selection genetic diversity. Moreover, identifying genetic variants in a single species can establish a representative seed collection for each evolutionary lineage. In efforts to reach a resistant ecosystem in the face of environmental changes, it is necessary to include plant populations with high genetic diversity (Aavik and Aveliina 2018) and incorporate gene-level biodiversity in this context to produce practices with long-term success. Another line is the realization of transplant experiments and quantitative trait analysis for potentially adaptive variants, considering and measuring the performance of such populations in conditions not currently experienced by the species but expected in the future under global warming. These studies also constitute a gap for plants from *Campos Sulinos*. The ability to rapidly adapt to changing environments is linked to the genetic and demographic traits of the species. Thus, understanding the several processes involved in microevolution would increase short and long-term success of conservation and restoration efforts. We live in the UN Decade on Ecosystem Restoration, and the scientific community argues the importance of including genetic diversity in such efforts. Unfortunately, for the *Campos Sulinos*, there is a considerable gap in knowledge on intraspecific genetic diversity for plant species.

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Chapter 10
Birds of the *Campos Sulinos*

Glayson A. Bencke, Rafael A. Dias, and Carla Suertegaray Fontana

10.1 Introduction

This chapter reviews and summarizes the existing knowledge on the diversity, distribution patterns, life history, ecology and conservation of birds in the *Campos Sulinos* of southern Brazil, with a focus on grassland species. It is intended to provide a contextualized view of the most relevant topics rather than an in-depth analysis of each aspect, combining published information and the personal experience of the authors. The chapter is divided into five main sections. Section 10.2 addresses grassland bird species diversity and endemism in the *Campos Sulinos*, and proceeds with a discussion of what grassland birds are and what are their main physical and behavioral adaptations. This section closes with an overall description of the spatial distribution patterns of open habitat species in the *Campos Sulinos* and an overview of regional and global conservation priorities. Section 10.3 deals with ecological and natural history aspects, such as the responses of bird communities to habitat structure, migration ecology and reproductive biology. Section 10.4 looks at the effects of land use patterns on grassland avian communities in the *Campos Sulinos*,

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focusing on agriculture, forestry, livestock grazing and fire as the main drivers of environmental change. Section 10.5 briefly describes the main threats facing grassland birds in the *Campos Sulinos* and assesses the role of protected areas and private lands in their conservation. The final section identifies research priorities to fill in some significant gaps in our knowledge on the *Campos Sulinos* grassland birds and their habitats.

10.2 Diversity and Composition

10.2.1 Overall Diversity

Worldwide, grasslands support specialized avian communities that are phylogenetically, ecologically and behaviorally diverse (Vickery et al. 1999; Maphisa et al. 2016; Lele et al. 2020; Li et al. 2022). The *Campos Sulinos* south-temperate grasslands of South America are no exception. In this region, at least 114 native bird species are adapted to a greater or lesser degree to grass-dominated ecosystems and regularly use grasslands for breeding, migrating, or wintering (see Appendix; Parker et al. 1996; Vickery et al. 1999; Azpiroz et al. 2012; Fontana and Bencke 2015). Two additional grassland species are now extinct in the *Campos Sulinos* and another 11 occur only as vagrants (Azpiroz et al. 2012; Fontana and Bencke 2015). In addition, a broad array of common open-country birds and habitat generalists, including some 52 species, range widely in the *Campos Sulinos* grasslands, not to mention dozens of waterbird, marsh, shrubland, edge and even forest species that occupy discrete patches of their preferred habitats amid open grassy landscapes (Stotz et al. 1996).

Common grassland birds of the *Campos Sulinos* include the flightless Greater Rhea (*Rhea americana*), the largest bird in the Americas, as well as such iconic and culturally significant species as the Southern Lapwing or *quero-quero* (*Vanellus chilensis*), the Chimango Caracara or *chimango* (*Milvago chimango*), the Rufous Hornero or *joão-de-barro* (*Furnarius rufus*) and the Chalk-browed Mockingbird or *calhandra* (*Mimus saturninus*), which have inspired music and other popular expressions in southern Brazil for centuries. Tinamous, raptors, shorebirds, Neotropical ovenbirds, tyrant flycatchers, pipits, New World blackbirds, and a variety of finch-like tanagers are also characteristic of these grasslands. Diversity is high across multiple trophic levels, and the most species-rich families are Thraupidae (20 species), Tyrannidae (15 species), Icteridae (10 species), Furnariidae (9 species) and Accipitridae (8 species), which include specialized groups such as *Alectrurus* tyrant flycatchers, grass-finches (*Emberizoides* spp.) and *capuchino* seedeaters (*Sporophila* spp.), among others.

The two grassland bird species considered extinct in the *Campos Sulinos* are the Dwarf Tinamou (*Taoniscus nanus*) and the Pampas Meadowlark (*Leistes defilippii*). Both are known in the *Campos Sulinos* only from nineteenth-century records on opposite edges of the region, from the *Campos Gerais* of northeastern Paraná, in the transition with the Cerrado (Straube et al. 2004; Uejima and Bornschein 2014) and from the southern coastal plain of Rio Grande do Sul, toward the Uruguayan border (Collar et al. 1992). The Pampas Meadowlark is thought to have been a rare winter visitor in southern Brazil, which ceased to occur after extensive contraction of its former range in the Argentine *pampas* during the early twentieth century (Tubaro and Gabelli 1999). The same may have happened with the Strange-tailed Tyrant (*Alectrurus risora*), of which the population that formerly inhabited the province of Buenos Aires in Argentina is known to have exhibited seasonal movements but is now extirpated (Collar et al. 1992). However, this striking flycatcher has recently made its long-awaited reappearance in the *Campos Sulinos* in two widely separated areas of Rio Grande do Sul, more than a century after its last known record (see de Melo et al. 2021). It is therefore best considered a vagrant.

Although bird species richness in grasslands is not especially high compared to other terrestrial ecosystems, the avifauna of the *Campos Sulinos* stands out as particularly diverse when put into perspective. The number of grassland specialists (obligate grassland birds sensu Vickery et al. 1999) found in the region (50 species) is only slightly lower than that of North America, Mexico and the Caribbean combined (59 species) and represents 40% of the total for South America (124 species). For South Africa, where grasslands originally covered about 360,000 km^2, Harrison et al. (1994) list 98 grassland bird species, of which 32 are classified as ‘indicator species’, a concept nearly equivalent to Vickery et al.’s (1999) obligate grassland species. The *Campos Sulinos* thus support a greater variety of grassland birds and about 50% more grassland-restricted species compared to South Africa, although the former are part of a larger grassland system (the *Río de la Plata* grasslands) and the difference in size between regions prevents a more direct comparison. Even avian groups of Northern Hemisphere origin such as *Anthus* pipits (Voelker 1999) are relatively well diversified in the *Campos Sulinos*, with all five species present in the region occurring side by side in a restricted area of sandy mesic grasslands in the southern coastal plain of Rio Grande do Sul (G. Bencke, pers. obs.).

In contrast to this rich biodiversity, the degree of avian endemism is low in the *Campos Sulinos*, mainly because these grasslands have been variously connected to other grassland regions of the Neotropics in both ancient and more recent times (Norambuena and Van Els 2020). The only bird species truly endemic to this grassland system is the Long-tailed Cinclodes (*Cinclodes pabsti*), a montane specialist restricted to the highland meadows of the South Brazilian Plateau across the border between Rio Grande do Sul and Santa Catarina. However, both the recently described Tropeiro Seedeater (*Sporophila beltoni*) and the Black-bellied Seedeater (*S. melanogaster*) have their small breeding ranges entirely within the *Campos Sulinos* and are thus “seasonal” endemics. Moreover, the subspecies *intermedia* of the Greater Rhea, though poorly differentiated, is largely confined to the *Campos Sulinos*, extending only a little further south into Uruguay (Kirwan et al. 2021).

Long-distance migrants are everywhere in the *Campos Sulinos* and represent about 30% of the species diversity, if vagrants are counted (Appendix; Azpiroz et al. 2012). They comprise non-breeding visitors from North America (e.g., Upland Sandpiper *Bartramia longicauda*) or southern South America (e.g., Rufous-chested

Dotterel *Charadrius modestus*), as well as a number of species that breed in the *Campos Sulinos* and move north within the Neotropics during austral fall and winter (Azpiroz et al. 2012). Yet, it was only over the past 10 years that ornithologists began to unravel some basic aspects of the migration of one of the most common and popular grassland passerines that breed in the *Campos Sulinos*, the Fork-tailed Flycatcher (*Tyrannus savana*; Jahn et al. 2013). This highlights how much remains to be learned about the ecology of bird migration in the south-temperate grasslands of South America (Tuero et al. 2019; see the Sect. 10.3.2 below).

Because grasslands are disturbance-dependent ecosystems that are inherently dynamic in space and time, the composition of grassland bird assemblages varies greatly at relatively fine scales (Wilsey et al. 2019). Grassland birds differ in their habitat requirements for vegetation cover and structure (Fig. 10.1), with some specialized species selecting areas of uniform short grass (e.g., Buff-breasted Sandpiper *Calidris subruficollis* and Short-billed Pipit *Anthus furcatus*) or tall grass (e.g., Wedge-tailed Grass-Finch *Emberizoides herbicola* and Grass Wren *Cistothorus platensis*) for nesting, foraging and cover, while others have less stringent habitat requirements and tolerate a wide variation in key environmental factors (e.g., Fork-tailed Flycatcher and Rufous-collared Sparrow *Zonotrichia capensis*).

Fig. 10.1 Characteristic grassland and savanna-like physiognomies of the *Campos Sulinos* of southern Brazil, with examples of associated bird species. Left, top to bottom: short, heavily grazed grassland (Short-billed Pipit, *Anthus furcatus*); moderately grazed grassland with a two-layered structure (Grassland Sparrow, *Ammodramus humeralis*); tall grassland with very low intensity grazing (Grass Wren, *Cistothorus platensis*). Right, top to bottom: wet-mesic ("hygrophilous") grassland on low lying, saturated terrain (male Pearly-bellied Seedeater, *Sporophila pileata*); upland grassland with *Eryngium*-dominated boggy swales (male Black-and-white Monjita, *Heteroxolmis dominicana*); *Espinilho* parkland (Lark-like Brushrunner, *Coryphistera alaudina*). (Photos: G. A. Bencke, except Lark-like Brushrunner (Raphael Kurz) and environment images on right-hand side (from top to bottom, Jonas Rosoni, Adriano Becker and Jan Mähler Jr))

Therefore, individual species abundances vary greatly across vegetation structural mosaics as a result of species-specific life-history traits (Hovick et al. 2014), to the extent that two neighboring cattle ranches with diverging management histories or even two adjacent pastures under different disturbance regimes can support rather distinct grassland bird assemblages (Dias et al. 2017). Similarly, bird assemblage composition can change significantly over time following disturbance events and ecological succession in grasslands (Beal-Neves et al. 2020; see Sect. 10.3 below).

10.2.2 Grassland vs. Non-grassland Birds

What defines a grassland bird is not a simple question. Fundamentally, grassland birds are those that rely on grass-dominated habitats for nesting or any other key behavioral or physiological activity in their life cycle (Vickery et al. 1999; Azpiroz et al. 2012). However, while many grassland birds use grasslands year-round, others do so only seasonally (i.e., for part of their annual cycle). For example, Baird's Sandpipers (*Calidris bairdii*), Red Knots (*Calidris canutus*), Hudsonian Godwits (*Limosa haemastica*) and Lesser Yellowlegs (*Tringa flavipes*) regularly nest in some type of grassland habitat in the boreal and arctic zones of North America (Vickery et al. 1999), but rarely, if ever, use grasslands while wintering in the *Campos Sulinos*, except when these become flooded in unusually wet years (Belton 1994; Dias et al. 2014). Furthermore, a large proportion of grassland birds (roughly two-thirds in the grasslands of southeastern South America and three-quarters in South America as a whole) do not occur exclusively in grasslands but also use a range of other open habitats, including anthropogenic ones (Stotz et al. 1996; Azpiroz et al. 2012). As an example, the Lesser Grass-Finch (*Emberizoides ypiranganus*) nests in both dry grasslands and wet grassy swales in the highlands of the South Brazilian Plateau (Chiarani and Fontana 2015) but also occurs in sedge marshes with dense emergent vegetation in adjacent lowlands, where it nests too (Accordi and Hartz 2006). Several other grassland-associated species, including Blue-black Grassquit (*Volatinia jacarina*), Double-collared Seedeater (*Sporophila caerulescens*) and Long-tailed Reed Finch (*Donacospiza albifrons*), are commonly found in successional habitats with little or no grass cover like brushy edges of woodlands and marshes, roadside thickets and shrubby clearings, where they coexist with shrubland "specialists" such as Rufous-capped Antshrike (*Thamnophilus ruficapillus*), Spix's Spinetail (*Synallaxis spixi*) and Bran-colored Flycatcher (*Myiophobus fasciatus*). Similarly, the Burrowing Owl (*Athene cunicularia*) and the Common Miner (*Geositta cunicularia*), besides being widespread in the *Campos Sulinos* grasslands, also breed in sandy dune fields sparsely covered with short pioneer vegetation all along the south Brazilian littoral (Belton 1994). In another case, a number of species use grasslands in combination with other spatially contiguous habitats. Black-and-white Monjita (*Heteroxolmis dominicana*) and Saffron-cowled Blackbird (*Xanthopsar flavus*), for instance, forage primarily in well-drained grasslands and occasionally in pastures and cultivated fields but depend on intervening boggy swales or adjacent marshes with dense vegetation for nesting and roosting (Belton 1994; Bencke et al. 2003). Also, in southeastern South America alone, about half of all grassland bird species make some use of agricultural areas such as paddy rice fields and upland croplands as alternative habitats, including Greater Rhea, Upland Sandpiper and Yellowish Pipit *Anthus chii* (Azpiroz et al. 2012). Further complicating the definition of grassland birds, some grassland species use different habitats in different parts of their ranges (Vickery et al. 2000; Azpiroz et al. 2012). This is the case of Sulphur-bearded Reedhaunter (*Limnoctites sulphuriferus*) and Spectacled Tyrant (*Hymenops perspicillatus*), which are typically grassland birds in the *pampas* of Argentina (Isacch and Martínez 2001), but are restricted to wetlands in the *Campos Sulinos* (Belton 1994). Finally, grassland birds vary greatly in their degree of specialization or "ecological connection" to grassland habitats (Vickery et al. 1999). While some highly specialized species such as Spotted Nothura (*Nothura maculosa*), Grass Wren and Ochre-breasted Pipit (*Anthus nattereri*) only need the dominant graminoid stratum of grasslands to meet all their life history requirements and can live in pure grassy habitats lacking any extra structural components, other grassland birds make little or no direct use of grasses (e.g., vultures, swallows and *Molothrus* cowbirds), or require non-grassy elements like shrubs and trees for nesting (e.g., most diurnal raptors, Firewood-Gatherer *Anumbius annumbi* and Chalk-browed Mockingbird) or foraging (e.g., Vermilion Flycatcher *Pyrocephalus rubinus* and White Monjita *Xolmis irupero*).

As seen, there is no clear line dividing grassland and non-grassland birds. That is, no uni- or multidimensional criteria exist to objectively define grassland birds. Grasslands themselves subtly grade into other vegetation types along environmental gradients of shrub cover, vegetation height and moisture: defining where a grassland ends and another plant community begins along a transition zone is itself an arbitrary decision. Perhaps not surprisingly, certain species of birds seem to prefer precisely these transitional environments, like South American Snipe (*Gallinago paraguaiae*), which forages and nests in grassy areas with soft, permanently moist to soggy wet soil.

Despite these difficulties with the definition of what constitutes a grassland bird, ornithologists have attempted to classify grassland birds according to their dependence on grassland habitats. To put it simply, obligate grassland users (or specialists) are species that are uniquely adapted and therefore largely restricted to grasslands (Vickery et al. 1999). These specialized taxa avoid or make little use of other habitats, especially human-modified ones (Stotz et al. 1996). In addition, grassland-obligate birds tend to be area-sensitive and occur only in the largest habitat patches (Lockhart and Koper 2018; Pretelli et al. 2018). As these species are extremely dependent on grasslands, they are affected the most by habitat loss and are highly likely to disappear in the absence of the appropriate grassland habitats (Vickery et al. 1999; Azpiroz et al. 2012). Although there is a lack of uniformity in the use of this classification among authors, examples of obligate grassland birds include Long-tailed Cinclodes, Sharp-tailed Tyrant (*Culicivora caudacuta*), Bearded Tachuri (*Polystictus pectoralis*), Ochre-breasted Pipit and Tropeiro Seedeater.

Facultative grassland birds, in turn, make regular and extensive use of grassland habitats, but their relationship to grasslands is not mandatory as they can complete their life cycle in alternative habitats, such as wetlands, savannas, shrublands, dune fields, pastures, or croplands (Azpiroz et al. 2012). Because they are able to survive in a variety of open habitats, these species are often referred to as "generalist" grassland birds, and many are associated with the presence of a sparse to moderate woody cover (Askins et al. 2007). Overall, facultative grassland birds are little or not affected by fragmentation of grass-dominated habitats (Lockhart and Koper 2018), tolerate a wide range of habitat patch sizes (Pretelli et al. 2018; Silva and Fontana 2021), and are likely to be outcompeted by specialists in small grassland remnants as land use change intensifies (Staude et al. 2021). They are generally considered less sensitive to habitat loss than obligate grassland users. In the case of widespread loss of grassland habitats, these species would likely decline but not become extinct (Vickery et al. 1999; Azpiroz et al. 2012). As expected, there are more facultative than obligate grassland species and some familiar examples from the *Campos Sulinos* include Eared Dove (*Zenaida auriculata*), White-tailed Hawk (*Geranoaetus albicaudatus*), Rufous Hornero, White Monjita, Rufous-collared Sparrow and Blue-black Grassquit.

The distinctiveness and specialization of grassland avifaunas are reflected in the variety of adaptations that have evolved among grassland birds (Vickery et al. 1999). Ground nesting is a behavioral trait shared by more than 30% of the grassland birds that breed in the *Campos Sulinos* and, at least among species that can fly, likely evolved as an adaptation to reproduce in open environments with few or no trees (Collias 1964; Appendix). However, not all of these species place their nests level with the soil surface but instead hide them close to the ground within clumps of grass or other dense herbage, where they are kept well concealed from predators by overhanging vegetation (e.g., Grassland Yellow-Finch *Sicalis luteola* and Great Pampa-Finch *Embernagra platensis*). A few grassland generalists are quite versatile with regard to nest placement and nest on the ground only facultatively, like Eared Dove, Chimango Caracara and Rufous-collared Sparrow.

Aerial displays constitute another behavioral trait exhibited by a relatively high proportion of bird species in grassland ecosystems. Airborne sexual displays are more likely to evolve in open habitats than in closed forests because visual signals are transmitted more effectively and broadly with more intense illumination and fewer obstructions (Menezes and Santos 2019). Many grassland birds sing during their aerial displays and it has been suggested that singing in flight enhances the broadcast of auditory signals due to less attenuation away from the ground (Byers and Kroodsma 2016). In the *Campos Sulinos*, aerial displays are performed by at least 27 grassland species representing a wide variety of bird families and genera, from pigeons and nightjars to snipes, and from tyrant flycatchers to pipits and finches. These exhibitions range from the short, jerky jumps of the Chalk-browed Mockingbird, through the twisty courtship displays of the Fork-tailed Flycatcher, to the obstinate and almost endless song flights of the Short-billed Pipit. Elaborate aerial exhibitions, which in some species are accompanied by mechanical sounds produced by modified wing feathers, occur in the Sickle-winged Nightjar

(*Hydropsalis anomala*), Cock-tailed Tyrant (*Alectrurus tricolor*) and Bearded Tachuri, for example.

Camouflage is also a widespread adaptation. Many grassland birds, especially small-bodied ones, feature striped patterns of dark-colored streaks on light backgrounds in their upperparts (and often on the flanks and breast). These patterns break up their outlines and allow them to blend in with the tangle of grass and herb stems where they live, thus helping them hide from predators (Fig. 10.2). In the *Campos Sulinos*, as many as 24 species of grassland passerines from seven families show prominently striped plumages. These include Bay-capped Wren-Spinetail (*Spartonoica maluroides*), Chotoy Spinetail (*Schoeniophylax phryganophilus*), Sharp-tailed Tyrant, pipits (*Anthus* spp.), Grass Wren, Grassland Sparrow (*Ammodramus humeralis*), grass-finches (*Emberizoides* spp.), Long-tailed Reed Finch, female White-browed Meadowlark and juvenile Great Pampa-Finch, among others.

One of the most remarkable examples of specialization among grassland birds is illustrated by the nature of the materials selected for nest construction by certain seed-eating passerines. As recently revealed by detailed studies on the reproductive behavior of five of the seven species of *capuchinos* (*Sporophila* spp.) that breed in the *Campos Sulinos*, females of these tiny seedeaters build their small cup nests almost entirely of dry stems and seedless heads of native grasses (Fig. 10.3), which are delicately interlaced and bound together with spider webs (Rovedder and Fontana 2012; Franz and Fontana 2013; Vizentin-Bugoni et al. 2013; Freitas et al.

Fig. 10.2 Many small grassland birds of the *Campos Sulinos*, like this Wedge-tailed Grass-Finch *Emberizoides herbicola*, have contrasting striped plumage patterns that help them blend into their environment and make them less visible to predators. (Photo: G. A. Bencke)

Fig. 10.3 Female Chestnut Seedeater *Sporophila cinnamomea* (left) and its nest made of seedless dry stems of native grasses (right). (Photos: G. A. Bencke)

2018; Rosoni et al. 2020). While grasses of several native genera are used (e.g., *Paspalum*, *Agrostis*, *Sorghastrum*, *Axonopus*, *Eragrostis*, *Cinnagrostis*, *Chascolytrum*, *Eustachys*, *Digitaria*), exotic species (e.g., *Avena sativa*) and other plants (e.g., Cyperaceae) or materials (e.g., roots, dry leaves) are found only rarely and in very small proportions in these nests (e.g., Rosoni et al. 2020). Therefore, in addition to being stem-gleaner granivores highly specialized in the consumption of the tiny seeds of native grasses (Silva 1999; Bencke et al. 2003), *capuchino* seedeaters also appear to be largely or even completely dependent on native grasses for nesting. Larger *Sporophila* seedeaters (*coleiros* and *patativas*) add non-grass material to their nests more frequently and in greater quantities than the *capuchinos* (e.g., Ferreira and Lopes 2017; Rosoni et al. 2019), but the nest of the grassland-specialist Tropeiro Seedeater is made entirely of dry grass inflorescences (Repenning and Fontana 2019), thus matching the pattern found among the smaller species of the genus. So far as known, the two grass-finches (*Emberizoides* spp.) also typically build nests made exclusively with vegetative parts of native grasses (Di Giácomo 2005; Marini et al. 2014; Chiarani and Fontana 2015), though other grass-like plants may be used, at least locally (Rodrigues et al. 2009).

The physical and behavioral traits that have evolved or developed among grassland birds as adaptations to a grassland-dwelling lifestyle are not limited to those described above and also include, for example, large body size, cursorial habits (Vickery et al. 1999), an elongated tail to help with balance on unstable perches that sway in the wind (e.g., Sharp-tailed Tyrant, *Emberizoides* grass-finches, Long-tailed Reed Finch; Evans 1999), long tertials that cover the flight feathers in the folded wing and protect them from abrasion against vegetation (Sick 1997), and a tendency, within certain families (e.g., Thraupidae), for species that live in open and sunny habitats to have more extensive preformative (i.e., post-juvenile) molts than their closed-habitat relatives as a way of compensating for increased plumage wear from daily exposure to sunlight and abrasive vegetation (Howell 2010; Guallar et al. 2021).

10.2.3 Distribution Patterns of Open Habitat Species

The contemporary configuration and historical dynamics of open landscapes in the Neotropics have a deep influence on the distribution of grassland birds in the *Campos Sulinos* (Van Els et al. 2019). Neotropical grasslands are not continuously distributed today and constitute a mosaic, but multiple lines of evidence indicate that they were more extensive and interconnected during the past 1.5 Myr as a result of paleoclimatic variations (Norambuena and Van Els 2020). The absence of major geographical barriers in the recent past adds to the fact that grassland birds tend to have a high dispersal ability because natural disturbance regimes and seasonal climatic fluctuations force them to move across the landscape (Norambuena and Van Els 2020). This allows drawing a general profile of high gene flow, reduced speciation rates and a strong preponderance of wide-ranging species for most Neotropical grassland bird communities. In fact, no genus or family of birds is restricted to the *Campos Sulinos,* and 40% of the avian genera that occur in this region are represented in North America, north of Mexico. In addition, more than half (55%) of the grassland bird species found in the *Campos Sulinos* are widely distributed in the open areas of tropical and/or temperate South America, the Neotropics, or, in a few cases, the Americas (Appendix). Another expressive contingent of grassland birds in the region (23%) has their ranges centered on the Cerrado or across the diagonal of dry formations that stretches from northeastern Brazil into northern Argentina, which comprises the Caatinga, Cerrado and Chaco domains (Luebert 2021).

A set of 16 grassland-associated species, however, have their breeding ranges clustered in the grasslands of southeastern South America (SESA), which in addition to the *Campos Sulinos* also encompass the remainder of the *Río de la Plata* grasslands and the Humid Chaco grasslands of southeastern Paraguay and northeastern Argentina (Azpiroz et al. 2012). Some of these species range farther north into the Chaco and Pantanal (e.g., Plumbeous Ibis *Theristicus caerulescens* and Monk Parakeet *Myiopsitta monachus*) or westward into the Espinal of north-central Argentina (e.g., Freckle-breasted Thornbird *Phacellodomus striaticollis*), while five migratory *Sporophila* seedeaters spread over a broad area of the Cerrado and neighboring regions outside the breeding season. But six of the remaining species are entirely (Long-tailed Cinclodes, Black-and-white Monjita and Saffron-cowled Blackbird) or mostly (Bay-capped Wren-Spinetail, Hudson's Canastero *Asthenes hudsoni* and Brown-and-yellow Marshbird *Pseudoleistes virescens*) restricted to the SESA grasslands. Along with some other grassland and marsh birds, such as Curve-billed Reedhaunter (*Limnornis curvirostris*), Sulphur-bearded and Straight-billed Reedhaunters (*Limnoctites sulphuriferus* and *L. rectirostris*), Strange-tailed Tyrant and Pampas Meadowlark, these species support the recognition of the open ecosystems of southeastern South America as an area of bird endemism and a well-defined zoogeographic region within the Neotropics (Haffer 1985; Stotz et al. 1996). It is worth noting that six of these narrow-ranged species belong to five monotypic or exclusive genera,[1] which underscores the importance of this region as a center of phylogenetic endemism where geographically restricted and evolutionarily unique lineages emerged and have persisted over time (Straube and Di Giácomo 2007; Murali et al. 2021).

Unlike the southern part of the *Campos Sulinos* (i.e., the Brazilian Pampa), which stretches uninterruptedly across Uruguay toward east-central Argentina and forms a continuous and much larger region of sub-humid temperate grasslands, the highland grasslands of the South Brazilian plateau in northeastern Rio Grande do Sul, Santa Catarina and Paraná (*campos planálticos*) are arranged as disjunct enclaves mostly surrounded by Araucaria forest and weakly connected with the Cerrado to the north and with the northern part of the *Río de la Plata* grasslands to the south (Andrade et al. 2018). Spanning ~4.5 degrees of latitude, these enclaves are believed to have become isolated only recently following the expansion of moist forests along major river valleys and hillsides in the late Quaternary (Behling et al. 2009). For this reason, they all share a similar assemblage of grassland birds, although, due to the effect of latitude, the further north, the greater their compositional affinities with the Cerrado, and the further south, with the Brazilian Pampa (Straube and Di Giácomo 2007). The influence of the Cerrado is evidenced by the geographic distributions of some bird species typical of this domain that occur only marginally in the *Campos Sulinos*, where they are restricted to the *Campos Gerais* region in northeastern Paraná. These include Plumbeous Seedeater (*Sporophila plumbea*), Black-masked Finch (*Coryphaspiza melanotis*), Cock-tailed Tyrant and Ocellated Crake (*Micropygia schomburgkii*), among others. The northern part of the *Campos Gerais* also corresponds to the contact zone of Plumbeous and Tropeiro Seedeaters, two closely related species with parapatric breeding distributions that abruptly replace each other across a discrete gradient of habitat and elevation (Repenning and Fontana 2013). Copper and Pearly-bellied Seedeaters (*Sporophila bouvreuil* and *S. pileata*), until recently considered conspecifics, also segregate in the same region, albeit through a broader hybridization area that extends into southern São Paulo (Medolago et al. 2020). The congruence between the contact zones of these two pairs of species is thought to be correlated with the subtle and gradual transition of the Cerrado to the grasslands associated with the Araucaria forests of the South Brazilian Plateau (Repenning and Fontana 2013). A few other Cerrado species appear to be expanding southward into or across the *Campos Sulinos* in recent years and may become more widespread in the region in the near future (e.g., Yellow-bellied Seedeater *Sporophila nigricollis* and White-rumped Monjita *Xolmis velatus*; Franz et al. 2018). Toward the other extreme of the *campos planálticos*, the greater influence of the *Río de la Plata* grasslands is demonstrated by a number of southern species that are relatively common in the highland grasslands of northeastern Rio Grande do Sul and adjacent Santa Catarina but are absent from or barely reach the northern sector of the *Campos Sulinos* in Paraná (e.g., Saffron-cowled Blackbird, Freckle-breasted Thornbird and Straight-billed Reedhaunter).

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[1] *Spartonoica*, *Limnornis*, *Limnoctites*, *Heteroxolmis* and *Xanthopsar*.

As a notable exception to the trend toward reduced speciation rates that characterizes modern grassland bird lineages in the Neotropics, southern *capuchino* seedeaters constitute a very recent and explosive avian radiation showing remarkably low levels of ecological and genetic differentiation and considerable interspecific gene flow (Campagna et al. 2012; Turbek et al. 2021). According to genetic data, the process of diversification of the southern *capuchinos* is ongoing and began as recently as the middle Pleistocene about 420 kyr ago (Campagna et al. 2012). Of the ten species of southern *capuchinos*, seven breed or are likely to breed in the *Campos Sulinos*. They exhibit complex distribution patterns and partially overlapping breeding ranges centered on the SESA grasslands (Campagna et al. 2017). However, although predominantly sympatric in a geographical sense, they occupy spatially segregated and often disjunct breeding ranges that are in whole or in part mutually exclusive, so that only one or two species are usually found breeding syntopically in a given area. For example, Black-bellied Seedeater and Tawny-bellied Seedeater (*Sporophila hypoxantha*) breed closely together over most of the *Campos de Cima da Serra* north of Rio das Antas (Repenning et al. 2010), while Chestnut Seedeater (*S. cinnamomea*) is the only species of *capuchino* found nesting in most of the *Campanha Meridional* and *Serra do Sudeste* regions, in south-central Rio Grande do Sul. The Marsh Seedeater (*S. palustris*) responds to specific environmental variables that do not appear to be significantly associated with the presence of other species, such as terrain wetness (Dias et al. 2023), and therefore is more likely to be found together with several other *capuchinos*, although segregating by habitat. Its breeding range overlaps with that of the Dark-throated Seedeater (*S. ruficollis*) and possibly also Rufous-rumped (*S. hypochroma*) and Pearly-bellied Seedeaters in the *Fronteira Oeste* region along the border with Argentina, and with that of the Chestnut Seedeater in the central trough along the upper Rio Negro in the border with Uruguay, but Marsh is the only breeding *capuchino* in the coastal marshes of southern Rio Grande do Sul. Finally, it has been shown that the seasonal distribution of some *capuchinos* is thermally limited and that temperature thresholds vary with the seasons, which allows us to hypothesize that seedeaters, in addition to being niche trackers that trace the fructification of grasses, are also climate niche shifters (Dias et al. 2023).

A vegetation type of particular ornithological and conservation interest embedded within the Pampa in the classification of Brazilian biomes by the Brazilian Institute of Geography and Statistics (IBGE 2004) is the *Prosopis–Vachellia* or *Espinilho* parkland of the extreme west of Rio Grande do Sul (Fig. 10.1). Although generally associated with the *Campos Sulinos*, this savanna-like formation of Chaco affinity is an extension of the Espinal ecoregion of adjacent Argentina and Uruguay. Several Chaco-related birds enter the Brazilian territory through this biogeographic insertion and together define a region with a unique bird composition in Brazil. Bird species nationally restricted to this limited sector of the *Campos Sulinos* include Brown Cacholote (*Pseudoseisura lophotes*), Tufted Tit-Spinetail (*Leptasthenura platensis*), Lark-like Brushrunner (*Coryphistera alaudina*), Chaco Earthcreeper (*Tarphonomus certhioides*), Little Thornbird (*Phacellodomus sibilatrix*), Short-billed Canastero (*Asthenes baeri*) and Yellow Cardinal (*Gubernatrix cristata*).

Several of these species are nationally threatened with extinction due to the marginal distribution of their habitat and shrinking populations in the country.

10.2.4 Threatened Birds of Open Habitats – Global and Regional Priorities

A total of 31 bird species from open-vegetation ecosystems in the *Campos Sulinos* are globally and/or nationally threatened or near-threatened (Table 10.1; ICMBio 2018; IUCN 2023). This represents around 20–30% of all bird species that are strict grassland taxa or rely on grasslands for key stages of their life cycle. Roughly 60% of these species are near-threatened or of least concern at the global level, while nationally this value decreases to 40%. The nine species that are red-listed nationally, but not globally, include grassland taxa with small regional populations that may be declining, such as Hudson's Canastero and Tawny-bellied Seedeater, as well as *Espinilho* birds that are common in Argentina and Uruguay but have tiny populations in Brazil (Serafini 2013; ICMBio 2018). Sharp-tailed Tyrant and Chestnut Seedeater are classified as threatened at the global but not at the national level due to updated regional distribution information used in the Brazilian assessment (ICMBio 2018). Novel data regarding distribution and population trends have led to the formal classification of the Black-bellied Seedeater as a threatened species in Brazil (ICMBio 2018).

There are a number of additional open-vegetation bird species that face local conservation issues in the *Campos Sulinos* but that do not extend to broader spatial scales. For example, Giant Snipe (*Gallinago undulata*) is classified as not threatened/Least Concern on the IUCN Red List and in Brazil, but is listed as threatened in all three states of the *Campos Sulinos*. This wetland resident is found in small, localized populations within grassy marshes in the highland grasslands of the South Brazilian plateau and in a few areas of the Brazilian Pampa. White-rumped Tanager (*Cypsnagra hirundinacea*), a Cerrado bird, and Plumbeous Seedeater are also classified as Least Concern both globally and nationally but are highly threatened within the *Campos Sulinos*. The former is possibly already extinct, while the latter persists in small numbers in the Cerrado contact zone. The Grass Wren and Freckle-breasted Thornbird exhibit yet another local threat pattern. Both are included in the Red Lists of Paraná and Santa Catarina because they face extinction in the highland grasslands of these states. However, in Rio Grande do Sul, where their ranges and populations are larger, these species are considered near-threatened and of least concern, respectively.

Seven globally and/or nationally threatened or near-threatened species in the *Campos Sulinos* occur in savanna or savanna-like habitats. These include *Espinilho* specialists such as Lark-like Brushrunner and Brown Cacholote, which are restricted to the westernmost part of the Brazilian Pampa. Yellow Cardinal, which is currently

Table 10.1 Globally (G) and/or nationally (N) threatened and/or near-threatened open-vegetation bird species of the *Campos Sulinos*

Species	G, N	Threats	Protected areas
Alectrurus tricolor	VU; VU.	2.1–3; 7.1; 8.1; 9.3.	Cer?; Gua?; VV?
Anthus nattereri	VU; VU.	1.3; 2.1–3; 3.3; 7.1; 8.1–2; 9.3.	AS-SG; BM; Cer?; CG?; CP; Gua; Pal?; SJ?; Tainh; VV.
Asthenes hudsoni	NT; VU.	1.1; 1.3; 2.2–3; 3.3; 6.1; 8.1.	LP; Taim?
Calidris subruficollis	NT; VU.	2.2–3; 3.3; 7.1; 8.1; 9.3; 11.4.	BM; LP; MG; SD; Taim.
Cinclodes pabsti	NT; NT.	2.1–2; 8.1.	Ara; AS-SG; SF; SJ; Tainh.
Circus cinereus	LC; VU.	1.1; 2.2; 3.3; 4.2; 7.1–2; 8.1; 9.3.	BM; BP; Esp; Ibira; LP; MG; SD; Taim.
Coryphaspiza melanotis	VU; EN.	2.1–3; 7.1; 8.1.	Cer?
Coryphistera alaudina Burmeister, 1860	LC; CR.	2.1; 2.3; 5.3.	Esp.
Culicivora caudacuta	VU; LC.	2.1–3; 7.1; 8.1.	Cax?; Cer?; CG; Gua; Ibira?; Ibiti?; VV.
Drymornis bridgesii (Eyton, 1849)	LC; NT.	2.1; 2.3; 5.3.	Esp.
Gubernatrix cristata (Vieillot, 1817)	EN; CR.	2.1–3; 5.1; 5.3; 6.1.	Esp.
Hydropsalis anomala	NT; NT.	1.1–2; 2.1–3; 3.2–3; 4.1; 7.1–2; 8.1; 9.1–3.	BP; Cax?; Cer?; CG?; CP; Gua; Irat?; TB?; VV.
Leptasthenura platensis Reichenbach, 1853	LC; CR.	2.1; 2.3; 5.3.	Esp.
Limnoctites rectirostris (Gould, 1839)	NT; NT.	2.1–3; 3.3; 7.1–2; 8.1; 9.3.	Ara; AS-SG; BP; CP?; MG; pod?; SF; Tainh.
Neothraupis fasciata (Lichtenstein, 1823)	NT; LC.	2.1–3; 7.1; 8.1.	Cer?; Gua?
Polystictus pectoralis	NT; NT.	2.1–3; 7.1; 8.1.	Esp; Gua; LP.
Pseudoseisura lophotes (Reichenbach, 1853)	LC; VU.	2.1; 2.3; 5.3.	Esp.
Rhea americana	NT; LC.	2.1–2; 3.3; 4.1; 5.1; 7.1; 8.1; 9.3.	Cer?; Esp; Ibira; LP; MG; SD; Taim.
Scytalopus iraiensis Bornschein, Reinert & Pichorim, 1998	EN; EN.	1.1–2; 2.1–2; 3.2; 4.1; 7.1–2; 8.1; 9.1–3.	AS-SG; BM; BP; CP; Irat; TB; VV.
Spartonoica maluroides	NT; LC.	1.1–2; 2.1; 2.3; 3.3; 7.1; 8.1.	BM; BP; Ibira?; LP; MG; Taim.
Sporophila beltoni	VU; VU.	2.1; 2.2; 5.1; 7.1–2; 8.1.	Cer?; CG; Gua; Ibiti?; Tainh; VV.

(continued)

Table 10.1 (continued)

Species	G, N	Threats	Protected areas
Sporophila cinnamomea	VU; NT.	2.1; 2.2; 2.3; 7.2.	Cer; Gua?; Ibira?; MG; SD.
Sporophila hypochroma	NT; LC.	2.1–3.	Esp; Tainh.
Sporophila hypoxantha	LC; VU.	2.1–2; 5.1; 7.1–2; 8.1.	Cax?; Cer; CP; Esp; Gua; Ibiti; Irat?; SD; SJ; TB?; VV.
Sporophila melanogaster	NT; VU.	2.1–2; 5.1; 7.1–2; 8.1.	AS-SG; Cer?; CP; Gua; Irat?; SF?; SJ; Tainh; VV?
Sporophila palustris	EN; VU.	2.1–3; 3.3; 4.2; 8.1.	BM; Esp; Ibira?; MG; SD; Taim?
Sporophila pileata	LC; NT.	2.1–3; 5.1; 7.1–2; 8.1; 9.3.	AS-SG?; BP; Cer; Gua; Ibira?; SD; VV.
Sporophila ruficollis	NT; VU.	2.1; 2.3.	Esp.
Urubitinga coronata	EN; EN.	2.1–2; 3.3; 4.2; 5.1; 8.1; 9.3.	AS-SG; Cer?; CP?; Gua; Ibiti; SJ; SF; Tainh; VV.
Xanthopsar flavus	EN; VU.	2.1–3; 7.1–2; 8.1–2; 9.3.	Ara; A-E?; AS-SG; BP; Ibiti?; Pod; SD?; SJ?; SF?; Tainh.
Heteroxolmis dominicana	VU; VU.	2.1–3; 3.3; 7.1–2; 8.1–2; 9.3.	Ara; A-E?; AS-SG; BM; BP; Cer?; CP; Gua; Irat?; LP; Pal?; Pod?; SF?; SJ; Taim; Tainh; VV.

Sequential threats within the same threat level are indicated with hyphens (e.g., 2.1–3 includes types 2.1, 2.2 and 2.3). Protected areas where the presence of a species requires confirmation are denoted by question marks. See Appendix for common English names and authorship of grassland species

IUCN Red List Categories: LC- Least Concern; NT- Near Threatened; VU- Vulnerable; EN- Endangered; CR- Critically Endangered

Level-2 IUCN threat types: 1.1- Housing & Urban Areas; 1.2- Commercial & Industrial Areas; 1.3- Tourism & Recreation Areas; 2.1- Annual & Perennial Non-Timber Crops; 2.2- Wood & Pulp Plantations; 2.3- Livestock Farming & Ranching; 3.2- Mining & Quarrying; 3.3- Renewable Energy; 4.1- Roads & Railroads; 4.2- Utility & Service Lines; 5.1- Hunting & Collecting Terrestrial Animals; 5.3- Logging & Wood Harvesting; 6.1- Recreational Activities; 7.1- Fire & Fire Suppression; 7.2- Dams & Water Management/Use; 8.1- Invasive Non-Native/Alien Species/ Diseases; 8.2- Problematic Native Species/Diseases; 9.1- Domestic & Urban Waste Water; 9.2- Industrial & Military Effluents; 9.3- Agricultural & Forestry Effluents; 11.4- Storms & Flooding

Protected areas: Ara- Aratinga State Park; A-E- Aracuri-Esmeralda Ecological Station; AS-SG- Aparados da Serra and Serra Geral National Parks (contiguous); BM- Banhado do Maçarico Wildlife Refuge; BP- Banhado dos Pachecos Wildlife Refuge; Cax- Caxambu State Park; Cer- Cerrado State Park; CG- Campos Gerais National Park; CP- Campos de Palmas Wildlife Refuge; Esp- Espinilho State Park; Gua- Guartelá State Park; Ibira- Ibirapuitã Biological Reserve; Ibiti- Ibitiriá State Park; Irat- Irati National Forest; LP- Lagoa do Peixe National Park; MG- Mato Grande Biological Reserve; Pal- Palmas State Park; Pod- Podocarpus State Park; SD- São Donato Biological Reserve; SF- São Francisco de Paula National Forest; SJ- São Joaquim National Park; Taim- Taim Ecological Station; Tainh- Tainhas State Park; TB- Três Barras National Forest; VV- Vila Velha State Park restricted to a single population occupying the Espinilho State Park and its surroundings, was widely distributed along the Uruguayan border until the mid-twentieth century (Serafini 2013). Chaco Eagle (*Urubitinga coronata*) occurs mostly in Araucaria Forest-grassland mosaics in the *campos planálticos* (ICMBio 2018). This eagle exhibits low population densities and relies on large wilderness areas to sustain viable populations (ICMBio 2018). The largest populations in the *Campos Sulinos* occur in the *Campos Gerais* region and in the headwaters of the Rio Uruguai in southeastern Santa Catarina and northeastern Rio Grande do Sul. The White-banded Tanager (*Neothraupis fasciata*), another savanna bird of regional conservation concern, was recorded only in the Cerrado contact zone in northern Paraná and has not been reported recently from this region (BirdLife International 2023).

Five other species of global and/or national conservation concern in the *Campos Sulinos* are associated with wetlands. These species inhabit dense, grassy marshes with saturated or lightly flooded soils, whether in river floodplains, peat bogs, along drainage lines in undulating terrain, or on the edges of other wetland types (Serafini 2013; ICMBio 2018). Due to the spatial configuration of their habitat, they tend to have naturally small, isolated populations but can attain high densities in some places (Serafini 2013; ICMBio 2018). The Marsh Tapaculo (*Scytalopus iraiensis*) and Sickle-winged Nightjar are found in a number of localities in the highland grasslands of the South Brazilian Plateau, especially in Paraná, plus a few wetlands in central and eastern Rio Grande do Sul (Serafini 2013; BirdLife International 2023). The Straight-billed Reedhaunter is exclusively found in marshes dominated by the spiny Giant Sea Holly (*Eryngium pandanifolium* and *E. chamissonis*), with the largest populations occurring in Rio Grande do Sul, namely in the highland grasslands and the *Serra do Sudeste* region (Serafini 2013). The Cinereus Harrier (*Circus cinereus*) and Bay-capped Wren-Spinetail occur throughout the Brazilian Pampa (Serafini 2013; ICMBio 2018). The former has a large range and forages over a variety of open habitats, but its breeding population is small and restricted to a few localities with sawgrass marshes, especially in the southern coastal plain (ICMBio 2018). The Bay-capped Wren-Spinetail breeds in the saltmarshes of Lagoa do Peixe and the Lagoa dos Patos estuary, where it can attain high densities, and also in lightly flooded grassy areas within freshwater marshes along the coastal lagoons (Serafini 2013). During the winter, it appears to use inland grasslands more frequently, possibly due to the presence of dispersing individuals or an influx of migratory populations from neighboring countries (Serafini 2013).

The 19 remaining species of conservation concern are grassland taxa and have variable distributions in the *Campos Sulinos*. Three of these, the Long-tailed Cinclodes, Black-bellied Seedeater and Tropeiro Seedeater, are entirely or seasonally restricted to the highland grasslands of southern Brazil. The first is thought to be experiencing a moderate population decline (BirdLife International 2023). It inhabits open short-grass grasslands, usually with rocky outcrops, and may occur even near human habitations (BirdLife International 2023). The two seedeaters are widespread in highland grasslands and are found in areas with tall, dense grasses, forbs and small bushes (Serafini 2013; ICMBio 2018). The Black-bellied Seedeater prefers grassy marshes in drainage swales, whereas the Tropeiro Seedeater occurs in drier grasslands on steep terrain (Serafini 2013; ICMBio 2018). Important areas for the latter include the highest sectors of the *Campos Gerais* and the grasslands along the headwaters of the Rio Pelotas/Uruguai in southeastern Santa Catarina and northeastern Rio Grande do Sul (Serafini 2013; ICMBio 2018).

Seven grassland species occur both in the highland grasslands and in the Brazilian Pampa. Tawny-bellied Seedeater and Ochre-breasted Pipit are more common in the highlands, whereas Bearded Tachuri is more widespread in the Pampa. Sharp-tailed Grass-Tyrant, Saffron-cowled Blackbird, Black-and-White Monjita and Pearly-bellied Seedeater have important populations in both regions.

Tawny-bellied Seedeater uses grassy marshes in drainage lines and also drier grasslands on steep terrain (Serafini 2013; ICMBio 2018). The population of this species is decreasing, and its survival depends on large, well-preserved grassland habitats (Serafini 2013; ICMBio 2018). Key conservation areas include the westernmost sectors of the *Planalto Médio* in north-central Rio Grande do Sul, the highland grasslands of northeastern Rio Grande do Sul and southeastern Santa Catarina, and the lower reaches of the *Campos Gerais* (Serafini 2013; ICMBio 2018).

Ochre-breasted Pipit also relies on large, open grasslands (Serafini 2013; ICMBio 2018). This species prefers well-drained, grazed grasslands with short grass and mid-sized herb tussocks without shrubs or trees (Serafini 2013; ICMBio 2018; Fig. 10.4). It may temporarily occupy regenerated grasslands but avoids cultivated pastures or plantations (Serafini 2013; ICMBio 2018). Its population is sparse and localized, with important strongholds in the highland grasslands of southeastern Santa Catarina and northeastern Rio Grande do Sul, in the *Campos de Água*

Fig. 10.4 Ochre-breasted Pipit *Anthus nattereri* in its typical habitat: moderately grazed upland grasslands without shrubs or trees. (Photo: G. A. Bencke)

Fig. 10.5 Male Saffron-cowled Blackbird *Xanthopsar flavus* foraging in a cornfield in the highlands of northeastern Rio Grande do Sul. (Photo: G. A. Bencke)

Doce–Palmas grasslands across the border of northern Santa Catarina and southern Paraná, and in the *Campos Gerais* region (Serafini 2013; ICMBio 2018).

Saffron-cowled Blackbird and Black-and-White Monjita occupy grasslands intermixed with *Eryngium* spp. and sawgrass marshes (Serafini 2013; ICMBio 2018). The blackbird can adapt to agricultural landscapes with small marshes and feed in planted pastures and row crops (Fig. 10.5), but the monjita is more dependent on extensive grasslands and rarely forages in plantations (Serafini 2013; ICMBio 2018). The monjita has a broader distribution in highland grasslands, whereas the blackbird is more widespread in the Pampa (Serafini 2013; ICMBio 2018). Significant populations of both species can be found in the highland grasslands of southeastern Santa Catarina and northeastern Rio Grande do Sul, as well as in the *Serra do Sudeste* region and adjacent central trough of Rio Grande do Sul along the upper Negro and Santa Maria rivers (Serafini 2013; ICMBio 2018). The *Planalto Médio* and *Planalto das Missões* are also important for the blackbird, while the southern littoral holds an expressive population of the monjita (Serafini 2013; ICMBio 2018).

Sharp-tailed Grass-Tyrant and Bearded Tachuri have small, isolated populations and may thrive in limited remnants of suitable habitat (Serafini 2013; ICMBio 2018). The *Campos Gerais*, the highland grasslands of southeastern Santa Catarina and northeastern Rio Grande do Sul, and the mid-western region of Rio Grande do Sul (*Campanha Central*) are important areas for the Sharp-tailed Grass-Tyrant (Serafini 2013; ICMBio 2018). The main strongholds for the Bearded Tachuri are the transitional zones between grassy marshes and drier grasslands in western Rio Grande do Sul (Serafini 2013; ICMBio 2018). Both species use wet and dry grasslands with dense grasses, as well as grasslands with scattered shrubs and forbs on gentle slopes (Serafini 2013; ICMBio 2018).

Pearly-bellied Seedeater has important populations in the *Campos Gerais* and in the northern, central and mid-western sectors of the Brazilian Pampa (Serafini 2013). It occurs in wet and dry grasslands, grassy marshes and grassy road edges, preferring habitats with tall grasses, sedges and scattered shrubs (Serafini 2013). This species may inhabit agricultural areas if small patches of suitable habitat are present in the landscape.

Within the *Campos Sulinos*, seven grassland species that are of conservation concern at the global and/or national level are restricted to the Brazilian Pampa. These include the Greater Rhea, which is extinct in the *Campos Gerais* but still occurs throughout most of the Pampa. The largest populations are found in the west, along the Uruguayan border, and in specific sectors of the coastal plain. This ground-dwelling bird displays a preference for open landscapes, particularly large natural grasslands characterized by low vegetation (BirdLife International 2023). However, rheas also use cultivated fields and revegetated grasslands, albeit at lower population densities (BirdLife International 2023). Despite still being present in relatively high numbers in large cattle-raising ranches and rice lands, the population of this species is believed to be declining globally (BirdLife International 2023).

Hudson's Canastero occurs in coastal grasslands with a mix of short and tall herbs along wetland margins or dunes (Serafini 2013). It has a small, apparently declining population and occurs only in a handful of localities in the *Campos Sulinos* (Serafini 2013). Buff-breasted Sandpiper is predominantly found in the southern coastal plain of Rio Grande do Sul, although there are scattered records in the central and western Pampa. This long-distance migrant shows a preference for open grasslands with very short grass, particularly along saltmarshes (ICMBio 2018; Faria et al. 2023a).

Chestnut, Rufous-rumped, Dark-throated and Marsh Seedeaters primarily inhabit natural grasslands, favoring areas with tall, dense grasses and forbs (Serafini 2013; ICMBio 2018). They are commonly found in wetter depressions and drainage swales, including *Eryngium* spp. marshes, but can also occur in drier contexts, particularly the Dark-throated Seedeater (Serafini 2013; ICMBio 2018). Marsh Seedeater prefers grassy marshes adjacent to large wetland areas (Serafini 2013; ICMBio 2018). Chestnut Seedeater is the most widespread species of the genus in the Brazilian Pampa, being absent only from the coastal and the northwestern sectors (Serafini 2013). Rufous-rumped Seedeater is rare, with a few confirmed sightings in western Rio Grande do Sul, but likely nests locally (M. Repennig, pers. comm.). Dark-throated Seedeater is primarily found in western Rio Grande do Sul, especially in the extreme west (Serafini 2013; ICMBio 2018). Marsh Seedeater is sparsely distributed from the border with Argentina to the southern coastal plain (Serafini 2013; ICMBio 2018). While natural grasslands are their preferred habitat, they can use small patches of tall grasses found along roadsides and on the edges of soybean and rice fields (Serafini 2013; ICMBio 2018). Important areas for these species include marshes and ricelands of western Rio Grande do Sul, the upper Rio Negro drainage, the southern and southeastern reaches of the *Serra do Sudeste*, and, for Marsh Seedeater, wetlands of the southern littoral (Serafini 2013; ICMBio 2018).

Cock-tailed Tyrant and Black-masked Finch have been recorded from a few locations in the *Campos Gerais* of northeastern Paraná and may be on the verge of extinction in the *Campos Sulinos*. These species inhabit grasslands with tall herbs, preferably without trees and tall bushes, and are restricted to minimally disturbed or undisturbed areas (Serafini 2013; ICMBio 2018).

10.3 Ecology and Natural History

10.3.1 Habitat Structure Relationships

The diversity of avian communities in grasslands is generally driven by variation in habitat structure (Fisher and Davis 2010; Azpiroz et al. 2012). In the *Campos Sulinos*, habitat features have a differential effect upon taxonomic alpha and beta diversity. Within grasslands, species richness may or may not differ between areas with distinct habitat features (Gressler 2013; Dias et al. 2017; Jacoboski et al. 2017; Becker et al. 2019; Silva et al. 2019; Beal-Neves et al. 2020; Silva and Fontana 2020). On the other hand, the composition of bird communities consistently changes with differences in habitat mediated by livestock grazing intensity, grazing exclusion, fire frequency and active restoration (Dias et al. 2017; Jacoboski et al. 2017; Becker et al. 2019; Chiarani et al. 2020; Silva and Fontana 2020).

Differences in vegetation height, vegetation patchiness, bare ground cover and presence of forbs and woody plants explain most of the variation in avian taxonomic beta diversity in the *Campos Sulinos* (Dias et al. 2014, 2017; Jacoboski et al. 2017; Silva et al. 2019; Beal-Neves et al. 2020; Chiarani et al. 2020; Silva and Fontana 2020). Vegetation height is particularly important, with 2–3 groups of species assembled according to the stature of prevailing grassland plants (Dias et al. 2014, 2017). Tall and short grass specialists occur, respectively, at the extremes of the height gradient, the first where plants are taller than 35–40 cm and the latter below 20–25 cm (Dias et al. 2014, 2017). No specialists of intermediate height were detected in the *Campos Sulinos*, but an array of generalists occur in grasslands with herbs 20–35 cm high, plus specialists from both extremes (Dias et al. 2014, 2017). Interspecific competitive exclusion and adaptive responses to climatic stress or predation risk are the main mechanisms behind the beta diversity-plant height gradient in grasslands (Fisher and Davis 2010; Dias et al. 2014). Bare ground and vegetation patchiness influence vigilance and foraging efficiency (Fisher and Davis 2010; Dias et al. 2014). Presence of non-grass forbs and woody vegetation provides nest sites, shade and food resources and enhances the diversity of non-grassland species (Dias et al. 2014; Beal-Neves et al. 2020; Silva and Fontana 2020).

Habitat effects on alternative facets of diversity have been far less explored. Time since fire influences community functional composition described by food guilds, but not alpha diversity, with granivores favoring sites with longer time since fire and taller vegetation (Beal-Neves et al. 2020). Grassland bird communities showed very diverse phylogenetic affinities, especially in the winter (Gianuca et al. 2014).

Despite the lack of phylogenetic clustering or overdispersion, different phylogenetic clades predominate in grasslands (Gianuca et al. 2014).

Most studies at the organism level have focused on characterizing the breeding habitat of passerines, with limited research investigating the relationship between individual organisms and their habitats across different life cycle stages. Nesting habitats were described for seedeaters (Rovedder and Fontana 2012; Franz and Fontana 2013; Repenning and Fontana 2016, 2019; Rosoni et al. 2019, 2020) and two thraupids (Chiarani and Fontana 2015; Beier and Fontana 2019). Plant height and nest concealment were important in affecting nest survival and the selection of breeding territories of seedeaters (Chiarani and Fontana 2015; Repenning and Fontana 2016; Rosoni et al. 2019). Microhabitat analysis showed that Southern Lapwings prefer areas with low vegetation height and some human impact, thus benefiting from altered environments (Delfino and Carlos 2021).

10.3.2 Migration Ecology

Twenty-eight species of long-distance migratory grassland birds regularly occur in the *Campos Sulinos* (Appendix). These comprise 15 breeding migrants (including no less than 10 *Sporophila* seedeaters), 12 non-breeding visitors (including five shorebirds) and a rare transient whose migratory route is mostly tangential to the *Campos Sulinos* (Bobolink *Dolichonyx oryzivorus*). Migratory grassland birds vary in size from the ~1-kg Swainson's Hawk (*Buteo swainsoni*) to the 8–10-g *capuchino* seedeaters (*Sporophila* spp.). According to the extent and geographic pattern of their annual migratory movements, the vast majority of these species fit into one of two main categories: (1) Nearctic-Neotropical migrants, which breed in the temperate grasslands or arctic tundra of North America and winter in the *Río de la Plata* grasslands of South America, and (2) Neotropical austral migrants, which breed at cool or temperate latitudes of South America and move to lower latitudes within the Neotropics in austral winter (Jahn et al. 2017). The latter category is further divided into (2.1) South American cool-temperate migrants, which breed in Patagonia and winter in south-temperate grasslands, and (2.2) South American temperate-tropical migrants, which breed in temperate latitudes and winter in the tropical grasslands of the Cerrado domain or further north in the Llanos (Joseph 1997; Jahn et al. 2020). A few Cerrado grassland birds that breed only marginally in the *Campos Sulinos* migrate mainly across the grasslands of tropical South America and are best classified as intra-tropical migrants (Jahn et al. 2017).

Migration patterns of Nearctic-Neotropical migrants that winter in the *Campos Sulinos* or pass through the region on their way to Argentina and Uruguay are better known. Both the Upland Sandpiper and the Buff-breasted Sandpiper use the Central Americas Flyway and undertake impressive journeys linking cold and temperate grasslands on different continents. Upland Sandpipers winter largely in native grasslands of rangelands used for livestock grazing in the Pampas and Campos ecoregions of Uruguay, Argentina and the southern part of the *Campos Sulinos*.

Satellite tracking of 15 individuals captured on their nesting grounds in U.S. revealed that they spent more time in non-breeding (39%) than in breeding areas (22%) and moved between centers of activity up to 400 km apart rather than settling in a single location during the northern hemisphere winter (Hill et al. 2019). Also, birds were capable of long non-stop flights of up to 5 days and 3758 km during southbound migration and up to 7 days and 7581 km during northbound migration, covering total distances of 12,467–20,904 km during their annual movements (Hill et al. 2019). Buff-breasted Sandpipers can cover even greater distances (>33,000 km) on their annual routes, which include important stopover sites in Colombia, Bolivia and Paraguay during the southbound migration through South America (Lanctot et al. 2016). Lagoa do Peixe National Park and Torotama Island, in the coastal plain of Rio Grande do Sul, hold high densities and globally significant concentrations of Buff-breasted Sandpipers and have been identified as key wintering sites for this near-threatened grassland shorebird within the *Campos Sulinos* (Lanctot et al. 2002, 2016; Faria et al. 2023a). Swainson's Hawks winter primarily in the *Río de la Plata* grasslands, but are notably scarce and sparsely distributed in the *Campos Sulinos*, where almost nothing is known about the species. However, several aspects of its winter ecology have been more intensively investigated over the past three decades after mass mortality events due to exposure to organophosphate insecticides affected the species on its main wintering range in Argentina (Kochert et al. 2011). Barn (*Hirundo rustica*) and Cliff (*Petrochelidon pyrrhonota*) Swallows are far more common in the *Campos Sulinos* as summer visitors from North America and may be locally abundant in coastal wetlands and inland agricultural areas, respectively. Populations of both species have recently "switched hemispheres" and successfully started to breed in their regular non-breeding range in Argentina, a remarkable life history reversal that resulted in novel migration strategies and entailed changes in their migratory, molting and breeding schedules (Winkler et al. 2017; Areta et al. 2021). Barn Swallows breeding in Argentina have rapidly changed their migratory movements and no longer return to North America on their annual migrations, now traveling no farther north than northern South America in the austral winter (Winkler et al. 2017). South American Cliff Swallows, in turn, may either return to North America for the austral winter or spend the non-breeding season in Mexico or northern South America, but do not breed in both hemispheres (Areta et al. 2021). Both species have been expanding their breeding ranges in South America and the Barn Swallow was recently observed nesting on the southern edge of the *Campos Sulinos* near the Uruguayan border (Almansa 2022), probably taking advantage of road bridges as nesting substrates (Winkler et al. 2017).

Cool-temperate migrants are present in the *Campos Sulinos* mainly between April and September and include Buff-winged Cinclodes (*Cinclodes fuscus*), Austral Negrito (*Lessonia rufa*), Black-crowned Monjita (*Nengetus coronatus*) and Chilean Swallow (*Tachycineta leucopyga*), among others (Belton 1994). Although the migratory movements and connectivity of austral migrants are still little studied, they have always been thought to come essentially from Patagonia. However, recent satellite tracking data unexpectedly revealed that three Rufous-chested Plovers tagged during the nonbreeding season in southern Brazil made non-stop flights of more than 2300 km over the southwestern Atlantic Ocean to reach their breeding grounds in the Falkland Islands (Faria et al. 2023b), thus uncovering a new migratory route in this migration system. As winter visitors, cool-temperate migrants are mostly restricted to the southern part of the *Campos Sulinos*, rarely venturing farther north in the non-breeding season, with the exception of Rufous-chested Plovers and Chilean Swallows, which often reach Paraná, southern São Paulo and even Rio de Janeiro.

Temperate-tropical migrants of the *Campos Sulinos* grasslands are exemplified by breeding passerines such as the Fork-tailed Flycatcher, which is classified as an intra-tropical migrant northward (Jahn et al. 2020). In the *Campos Sulinos*, the entire population of this species is migratory, as there are virtually no records of individuals remaining in the breeding areas during the austral winter. Fork-tailed Flycatchers arrive in late winter or early spring to breed and then depart between late January and late February to their wintering grounds primarily located within the Orinoco river basin in northern South America, flying during daytime at an average speed of 55 ± 9.8 km day^{-1} (data from birds tagged in Argentina; Jahn et al. 2013). Fork-tailed Flycatchers from both temperate-tropical and intra-tropical migratory populations may migrate directly to wintering grounds after breeding or make prolonged stopovers at intermediate sites during fall migration (Jahn et al. 2013, 2016), possibly to initiate flight feather molt (Jahn and Guaraldo 2018). The Vermilion Flycatcher likely exhibits a similar migratory pattern but is poorly studied. It is uncertain whether the individuals occasionally observed in the *Campos Sulinos* during the winter are breeding birds that failed to migrate or individuals in transit from other migratory populations.

The group of threatened *Sporophila* seedeaters of the *Campos Sulinos* is composed almost entirely of temperate-tropical migrants. These small to tiny passerines are year-long habitat specialists that track the fructification of grasses during migration (Jahn et al. 2017). Thus, they can follow circular routes linking multiple wintering areas that are used in different moments of the non-breeding season (Dias et al. 2023), much like hummingbirds that trace flowering resources while migrating. In sharp contrast to most Nearctic-Neotropical migrants that winter in the Southern Cone of South America, which vacate their extensive breeding grounds in the Northern Hemisphere to concentrate in relatively small areas of the Neotropics during the non-breeding season, *Sporophila* seedeaters disperse over large areas of north-central South America during the austral winter that are much larger than their small breeding ranges (Dias et al. 2023). A few species migrate entirely within Brazil, as is the case of the Tropeiro and Black-bellied Seedeaters, which breed in the *Campos Sulinos* and spend the winter in southeastern and central-western Brazil (Repenning and Fontana 2013; Dias et al. 2023). Because they do not cross national boundaries during migration, these species are not covered by international agreements such as the Memorandum of Understanding (MoU) on the Conservation of Southern South American Migratory Grassland Bird Species and their Habitats, supported by the Convention on Migratory Species (CMS), an initiative of the governments of Argentina, Bolivia, Paraguay and Uruguay, with Brazil as a signatory. Other species, however, are included in this agreement, such as Chestnut and Marsh

Seedeaters, which have important breeding populations in the *Campos Sulinos*, but also occur as breeding or migratory species in other countries.

Although also included in the CMS, the Cock-tailed Tyrant and Saffron-cowled Blackbird make seasonal displacements that are less clear. The former is found in Paraná between October and January, presumably during the breeding season (Serafini 2013), but destination areas are unknown and the species may be only partially migratory or even nomadic (Marini et al. 2012). Saffron-cowled Blackbird is considered sedentary in Brazil (Somenzari et al. 2018) or more widely (Fraga and Sharpe 2020). However, it can be highly mobile in the non-breeding season, which may explain variations in abundance observed at the local scale (Mohr et al. 2017). For example, concentrations of over 200 individuals observed in April 2010 in a marshy area in northeastern Rio Grande do Sul completely disappeared the other day (C. Fontana, pers. obs.). Similarly, the Black-and-white Monjita is generally considered resident in reference sources but gathers in small flocks in April and May in the highland grasslands of Rio Grande do Sul (Fontana 1994) and regularly occurs as a winter visitor in the floodplains of the lower Jacuí and Gravataí rivers around Porto Alegre. In Argentina, pre-migratory flocking behavior has been reported for this species since the end of the nineteenth century (Barrows 1883) and it is considered migratory there (Sick 1997). Therefore, the available evidence suggests that the Black-and-white Monjita is at least partially migratory and that its seasonal movements may be entirely restricted to the temperate grassland zone of southeastern South America. The southern migratory subspecies of the Bearded Tachuri is listed in Appendix II of the CMS, although its movements have not been investigated to date and the species is considered non-migratory in Brazil (Somenzari et al. 2018). In the Brazilian Pampa, Bearded Tachuris are found year-round but there is some evidence of individuals passing through the region in February and March (C. Fontana and G. Bencke, pers. obs.; Felipe Bernardi, *in litt.*), which may originate from more southerly breeding areas.

The intra-tropical migrant Lesser Elaenia (*Elaenia chiriquensis*) spends the non-breeding season mainly in Amazonia and the Cerrado. Tracking data from the Cerrado population showed that it has low migratory connectivity. One of three individuals tracked in Brazil first headed south to a staging area in Santa Catarina, then northwest to a second wintering area in the vicinity of the Pantanal, and then northeast back to the breeding area, while a second individual wintered in the Caatinga (Guaraldo et al. 2021). However, migratory routes and overwintering areas of Lesser Elaenias that breed in the northern part of the *Campos Sulinos* may differ.

10.3.3 Breeding Biology

Information on reproductive life-history traits, including clutch size, parental care, offspring survival and fertility, is crucial to understanding the impact of environmental changes on bird populations (Martin et al. 2000; Duca and Marini 2014; Boyce et al. 2015). This knowledge also plays a vital role in formulating conservation strategies to safeguard endangered species. In the *Campos Sulinos*, information on the reproductive biology of grassland birds is highly variable across species and ranges from brief accounts of nesting-related aspects based on fortuitous observations (e.g., Belton 1994; Maurício et al. 2013) to detailed studies grounded in intensive fieldwork and robust methodology (e.g., Rovedder and Fontana 2012; Franz and Fontana 2013; Repenning and Fontana 2016; Beier and Fontana 2019; Chiarani and Fontana 2019; Rosoni et al. 2019, 2020, 2023; Larré et al. 2022).

The first comprehensive studies focused on species with previous legal hunting status and encompassed investigations on mating behavior and systems, recruitment characteristics, sex ratios and growth curve analysis of Spotted Nothura and Red-winged Tinamou *Rhynchotus rufescens* (e.g., Menegheti 1981, 1984, 1988; Menegheti et al. 1985). Key findings were that males exhibit simultaneous polygyny while females display sequential polyandry, potentially explaining the predominance of females due to the inversion of sexual roles and increased male mortality risks.

Codenotti (1997) investigated the reproductive phenology and biometry of nests, eggs and nestlings of Greater Rhea. The breeding season of this species spans from late August to late February and encompasses courtship, harem formation, egg laying, incubation, hatching and chick care phases. Codenotti (1997) also described in detail the unique breeding behavior of this bird, where males construct the nest, incubate the eggs laid by a harem of females and provide parental care for the offspring.

A large proportion of recent research efforts have focused on species of *Sporophila* seedeaters that breed in the *Campos Sulinos*, from which some clear patterns have emerged, including modal clutch sizes of two eggs, female-only nest-building and incubation regimes, biparental care of young and fledglings and selection of grasslands with tall, well-structured vegetation for establishing territories and as preferred nesting sites (e.g., Repenning and Fontana 2016; Chiarani and Fontana 2015; Rosoni et al. 2020). It is noteworthy that, prior to these efforts, some small species of this group were described as birds of weedy marshes and bogs (Belton 1994). However, new information from studies in protected areas where fire and grazing are excluded has shown that up to 50% of Black-bellied Seedeater nests are placed in dry upland grasslands when dense tallgrass vegetation is available around wet depressions (Rovedder and Fontana 2012; E. Chiarani and C. S. Fontana, unpubl. data). This suggests that nesting site selection may be more constrained by vegetation structure than soil wetness in this and other *Sporophila* species.

The Straight-billed Reedhaunter, Black-and-white Monjita, Lesser Grass-Finch and Saffron-cowled Blackbird had their reproductive biology studied in the highland grasslands (Fontana 1994; Toriani-Moura 2013; Chiarani and Fontana 2015; Larré et al. 2022). These species nest mainly in *Eryngium* marshes and boggy swales embedded in grassland landscapes, usually near the edges. Nesting success appears to be low (around 10%), as observed for the Straight-billed Reedhaunter in the highland grasslands (Larré et al. 2022), Vermilion Flycatcher in the *Espinilho* parkland and the colonial breeding Saffron-cowled Blackbird in the Brazilian

Pampa (Mohr et al. 2017), though observed nesting success of the latter at fledging stage in another colony of the Brazilian Pampa ranged from 31.8% to 36.3% in two successive breeding seasons (Dias and Maurício 2002). Of 10 nests of the Black-and-white Monjita recently monitored in highland grasslands, all were predated or abandoned (C. S. Fontana, unpubl. data). Ongoing studies on the breeding biology of the Bearded Tachuri and Sharp-tailed Tyrant similarly point to low rates of nest success and have revealed important differences in reproductive traits compared to populations of these species studied in the Cerrado (C. Aguiar, pers. comm.). Bearded Tachuri is polygamous in the *Campos Sulinos* and depends on relatively large territories (~5 ha) to breed (C. S. Fontana and M. Repenning, unpubl. data).

In the *Espinilho* parkland, a tiny remaining population of the highly endangered Yellow Cardinal has been shown to exhibit social monogamy, intra- and inter-season mate exchange, interbreeding of closely related individuals and an unbalanced ratio of male:female births in the population (1.5:1), traits that at least in part reflect the small size and high degree of isolation of this population (Beier et al. 2017; Beier and Fontana 2019). In addition, unlike other populations of the species studied in neighboring countries, the Brazilian population breeds cooperatively, with one or two helpers often assisting breeding adults in territory and nest defense, feeding nestlings, and taking care of fledglings (Beier et al. 2017). Parasitism by the Shiny Cowbird (*Molothrus bonariensis*), which affects one-third of nests in northeastern Argentina (Domínguez et al. 2015), is rare in this population and has not been identified as a major threat to other threatened birds in the *Campos Sulinos* (e.g., *Sporophila* spp. and Saffron-cowled Blackbird).

Petry and Fonseca (2005) investigated the clutch size and number of nestlings of Cattle Egrets (*Bubulcus ibis*) over two consecutive breeding seasons, reporting an estimated breeding success of 1.16 fledged young per nest in the first period and 0.99 in the second. Data on nest cavity characteristics, breeding season phenology, clutch size and egg/nestling morphology are available for American Kestrel (*Falco sparverius*; Viana and Zocche 2016) and Long-tailed Cinclodes (Zocche et al. 2021).

10.3.4 Trophic Ecology

Studying the trophic ecology of open-vegetation birds provides a comprehensive understanding of their ecological roles, interactions and responses to environmental changes, leading to more informed conservation and management decisions. Despite such importance, the trophic ecology of open-vegetation birds in the *Campos Sulinos* has been largely neglected and represents one of the least studied aspects of avian ecology in the region.

Initial studies focused on investigating the diet of the Spotted Nothura and Red-winged Tinamou, which were formerly subjected to legal hunting (Menegheti and Arigony 1982; Menegheti and Oliveira 1982; Sander 1982). The diet of the Monk

Parakeet, known for its consumption of cultivated grains and fruits, was also examined (Fallavena and Silva 1988; Dahlem 1994).

Another research line examined the diet of the Burrowing Owl and American Kestrel by analyzing regurgitated pellets (Scheibler and Christoff 2004; Zilio 2005; Bastian et al. 2008). Zilio (2005) found that both raptors exhibited seasonal variations in their diet preferences in coastal dunes. During summer and spring, they predominantly consumed Coleoptera, whereas Orthoptera were more common during cold seasons. In owl pellets, Hymenoptera and Araneae were prevalent during winter and spring, while kestrels consumed more spiders in summer and Hymenoptera in spring. The trophic niche overlap was high (67%) and varied across seasons.

A comparative analysis of the diet of four cuckoo species revealed that the Guira Cuckoo (*Guira guira*) had the most diverse diet, including large volumes of Orthoptera and Araneae (Repenning et al. 2009). Its diet consisted of amphibians, reptiles, birds, various grasshopper species and a single species of spider. Feeding preferences of Southern Lapwing, Buff-breasted Sandpiper and American Golden-Plover (*Pluvialis dominica*) were investigated on the coastal plain (Faria et al. 2018). These species showed a strong preference for consuming Coleoptera, resulting in a significant overlap in their trophic niches. The Buff-breasted Sandpiper exhibited the broadest trophic niche, while the American Golden-Plover had the broadest isotopic niche breadth (Faria et al. 2018). All species had generalist diets but showed some preference for specific prey types (Faria et al. 2018).

10.4 Effects of Land Use Patterns on Avian Communities

10.4.1 Agriculture

The effects of agriculture on grassland birds have been studied in different spatial contexts. At finer spatial scales, natural grasslands used for livestock raising have higher species richness and total abundance than grasslands sowed with exotic grasses and cultivated fields (Silva et al. 2015a; Fontana et al. 2016; Staude et al. 2021). Species of conservation concern attain higher densities in grasslands, whereas species abundant in soybean farms are generalists (Silva et al. 2015a).

At the landscape scale, bird incidence and abundance decline as soybean cover increases (Silva et al. 2015b). Grassland birds require at least 80% of grassland cover to maintain high abundances in soybean areas (Silva et al. 2015b). Irrespective of the yield, most species are negatively affected by soybean crops (Dotta et al. 2016). Increasing yields in some areas while reducing grazing to low levels in others may favor avian conservation (Dotta et al. 2016).

The abundance of grassland specialists in grassland remnants increases with agricultural cover, while the share of generalists in total abundance and total species richness decreases (Staude et al. 2021). This occurs because, as grasslands dwindle, specialists crowd in grassland remnants, whereas generalists gradually disappear as they can survive in other habitats (Staude et al. 2021). Grassland remnants among crops enable grassland birds to forage in soybean fields and can serve as temporary refugia for specialists (Silva et al. 2015b; Staude et al. 2021).

10.4.2 Silviculture

The effects of commercial silviculture on avian diversity have been relatively well explored in the *Campos Sulinos*. Taxonomic alpha diversity described by both species richness and heterogeneity indices is lower in eucalyptus plantations than in grasslands and riparian forests (Jacoboski et al. 2016a, b, 2019; Jacoboski and Hartz 2020). Analysis of taxonomic beta diversity revealed differences in communities from eucalyptus plantations, grasslands and forests (Dias et al. 2013; Jacoboski et al. 2016a). Species in tree plantations are predominantly generalists and comprise either a subset of the species in natural forests or a distinct assemblage according to the cover of forest in the landscape (Dias et al. 2013; Jacoboski et al. 2016a; Jacoboski and Hartz 2020; Pezda et al. 2021). Tree plantations apparently act as a barrier for grassland birds and homogenize bird composition in the landscape (Jacoboski et al. 2019; Pezda et al. 2021).

The landscape context affects the functional diversity of birds in eucalyptus plantations and adjacent natural habitats. Avian functional alpha diversity is higher in *restinga* forests than in eucalyptus plantations (Jacoboski et al. 2016b). Species traits in plantations represent a subset of those of *restinga* forest birds, suggesting that some ecological functions can be maintained in plantations (Jacoboski et al. 2016b). In grassland-dominated landscapes, functional alpha diversity was lower in riparian forests than in grasslands and tree plantations, while functional evenness was higher in eucalyptus plantations compared to natural habitats (Jacoboski and Hartz 2020). Riparian forests have higher functional redundancy and perhaps are functionally more stable (Jacoboski and Hartz 2020). Higher functional diversity in plantations may indicate functionally dynamic and less stable communities (Jacoboski and Hartz 2020).

Tree plantations reduce the evolutionary distinctiveness of grassland communities (Jacoboski et al. 2019). Beta diversity analysis revealed clades more associated with grassland vegetation and others with forests (Jacoboski et al. 2019). Avian lineages from riparian forests were more prone to colonize tree plantations, whereas grassland lineages were unfit to do so (Jacoboski et al. 2019). Conversion of grasslands into tree plantations may thus threaten the existence of evolutionarily distinct bird lineages and grassland specialists not adapted to colonize tree plantations (Jacoboski et al. 2019).

10.4.3 Livestock Raising

Livestock grazing affects grassland bird assemblages mainly by changing vegetation cover and structure. Although livestock grazing often has a detrimental effect on bird abundance and species richness, in ecosystems with an evolutionary history of grazing, such as grasslands, livestock can take on the ecological role of extinct native herbivores in preventing shrub encroachment and creating habitat heterogeneity (Barzan et al. 2021). Under this premise, it has now been widely recognized that traditional livestock ranching is not only compatible with the long-term maintenance of natural grassland ecosystems, but can also be beneficial for bird and other biodiversity conservation, especially when management practices and grazing intensities vary across the landscape (Overbeck et al. 2007; Develey et al. 2008; Bencke 2009; Derner et al. 2009). Conversely, the promotion of a constant and spatially uniform grazing pressure across rangelands diminishes the natural complexity of the system and benefits a limited suite of species, leading to biodiversity loss (Hovick et al. 2014).

In the *Campos Sulinos*, bird species richness does not vary significantly in pastures with high, moderate and low grazing intensity, but species composition changes under different levels of disturbance (Dias et al. 2017). Differentiation of communities mainly stems from substitution between tallgrass and shortgrass specialists along the disturbance gradient (i.e., via spatial turnover), indicating a high complementarity among sites with contrasting vegetation structure and pointing to horizontal niche differentiation as the main underlying mechanism through which bird diversity is enhanced and maintained in these grasslands (Dias et al. 2017). Species-specific foraging and nesting requirements determine the strength of association with either tallgrass or shortgrass habitats (Azpiroz and Blake 2016). Ecological associations with other habitat variables modulated by livestock grazing, such as vegetation patchiness and bare ground cover, have also been detected among grassland birds in southeastern South America (Isacch and Cardoni 2011; Azpiroz and Blake 2016).

Grasslands used for livestock production in the *Campos Sulinos* are generally not intensively managed and are dominated by native plants. A two-layer vegetation structure predominates throughout the region, with short herbs forming a grazed lower stratum and tussocks of unpalatable grasses, forbs and woody plants making up a sparse upper layer as a result of prevailing ranching practices and a “management to the middle” culture that is not particularly beneficial for birds (Dias et al. 2017). Yet, bird responses to grazing depend on habitat requirements and life-history traits, among other factors, so optimal grazing intensity varies by species and guild (Barzan et al. 2021). Buff-breasted Sandpiper and American Golden-Plover, two Nearctic migratory shorebirds that spend the non-breeding season in coastal areas of the *Río de la Plata* grasslands, are associated with heavily grazed, short-grass native pastures during the austral spring and summer (Lanctot et al. 2002; Isacch and Cardoni 2011; Fig. 10.6). Both species have a high probability of occurrence (>0.6) when grass height is between 2 and 5 cm, but

Fig. 10.6 The Buff-breasted Sandpiper *Calidris subruficollis* depends on heavily grazed natural pastures while wintering in the *Río de la Plata* grasslands of southeastern South America. (Photo: G. A. Bencke)

their density drops to near zero when grass becomes >8 cm tall (Aldabe et al. 2019). Therefore, a high grazing intensity is required to maintain suitable wintering habitats for these species (Aldabe et al. 2019). In contrast, most threatened grassland bird species of the *Campos Sulinos* require tall and dense grasslands in ungrazed or lightly grazed natural pastures to survive, including Sharp-tailed Tyrant, Bearded Tachuri and several *Sporophila* seedeaters (Azpiroz et al. 2012; Azpiroz and Blake 2016; Fontana et al. 2016). Prevailing stocking rates in the region (around 0.8 head per hectare) seem to cause too much disturbance for these declining tallgrass specialists (Fontana et al. 2016) and stocking densities of around 0.4 animal units per hectare have been suggested as more suitable to maintain grassland-restricted birds in the *Campos Sulinos* (Dotta et al. 2016).

However, thresholds between conservation and degradation, or between sustainable use and overuse, are still poorly understood in this grassland system. There is empirical evidence from the results of standardized grassland bird surveys carried out on a variety of livestock ranches across the Brazilian Pampa that factors such as paddock size and beef production system (cattle finishing vs cow-calf production) may interact with animal load to affect the suitability of bird habitats (*Alianza del Pastizal* unpublished reports). Large paddocks are more likely to be heterogeneous than small ones because of greater variety in topography and more uneven distribution of grazing pressure (Askins et al. 2007; Ribic et al. 2009), while systems focused on raising cows and calves seem to be associated with more complex grassland vegetation structures, possibly because ranching practices and/or grazing patterns of livestock in these systems result in greater accumulation of ungrazed biomass. Similarly, studies comparing the effect of different grazing systems (e.g., continuous, rotational, winter-only grazing) on grassland bird assemblages in other parts of the *Río de la Plata* grasslands have highlighted the importance of diversifying rangeland management schemes at the landscape scale to provide habitat for coexisting species with different habitat requirements and as a way to reconcile economic and conservation objectives (Isacch and Cardoni 2011; Pírez and Aldabe 2023).

10.4.4 Grassland Fires

Bird communities in grassland ecosystems consist of species with varying levels of tolerance and dependence on fire or other disturbance factors. This imperative is essential for establishing and sustaining a continuous structural gradient of vegetation within grassland ecosystems, encompassing undisturbed grasslands over multiple breeding cycles and incorporating recently burned areas or heavily grazed pastures (Parker and Willis 1997; Derner et al. 2009). The composition of the avifauna in the highland grasslands, where fire has been used for a long time, fits this general pattern (Bencke 2009).

A study comparing bird assemblages in highland grasslands found that 50% of species were shared between fire-free grasslands in protected areas and grasslands subject to annual fires in adjacent rangelands (Bettio 2017). Although there was no difference in taxonomic richness, significant differences in species composition were observed between the two treatments (Bettio 2017; M. Bettio and C. Fontana, unpubl. data). Long-tailed Cinclodes, Ochre-breasted Pipit and Saffron-cowled Blackbird, among others, were associated with short and recently burned grasslands and Black-and-white Monjita, Black-bellied Seedeater and Long-tailed Reed Finch with denser, unburned grasslands. The threatened Saffron-cowled Blackbird specifically selects grasslands that undergo frequent vegetation burning in this region, while actively avoiding less disturbed areas characterized by tall grasses (Petry and Kruger 2010).

Bird communities in highland grasslands exhibit changes in richness, abundance and composition over time, depending on the fire disturbance regime (Chiarani et al. 2020). In areas with occasional burns, significant changes occur in all diversity measures following the disturbance, but recovery to pre-disturbance conditions typically takes around 2 years (Chiarani et al. 2020). Annually burned and unburned areas also experience changes but only in a few diversity measures and with less consistent temporal patterns (Chiarani et al. 2020). Species-specific responses were observed, with some species becoming more frequent and abundant in recently burned areas with short grass cover (e.g., Southern Lapwing, Hellmayr's Pipit *Anthus hellmayri* and Grassland Sparrow; Chiarani et al. 2020). Conversely, other species were more associated with unburned years when vegetation is taller (e.g., Freckle-breasted Thornbird, Lesser Grass-Finch and Long-tailed Reed Finch; Chiarani et al. 2020). Interestingly, certain species associated with tall grasses may not immediately disappear from burned sites after a fire but rather concentrate in areas with tall vegetation, such as *Eryngium* bogs (Chiarani et al. 2020). Recently burned short grasslands provide habitat for species that were previously absent or less abundant (Chiarani et al. 2020).

Beal-Neves et al. (2020) demonstrated a linear decrease in bird abundance and taxonomic diversity with increasing time since fire. They also found that time since fire influences the relative contribution of different feeding guilds in the bird community. Thus, maintaining grassland patches with different disturbance regimes, characterized by varying fire frequencies, at the landscape level can maximize conservation benefits for bird species and functional groups (Beal-Neves et al. 2020).

Tallgrass specialists may require more tailored strategies. The assessment of breeding territories of the Lesser Grass-Finch and Black-bellied Seedeater revealed that the number of territories of both species decreased by half in the year of burning, but only the former returned to pre-burning values after 1 year. A similar effect was detected in the case of the Tropeiro Seedeater, in which territories decreased in number and doubled or tripled in size following burns (M. Repenning and C. S. Fontana, unpubl. data). Numbers of the Cock-tailed Tyrant also decrease after fires, but the species soon reappears with the regrowth of vegetation (Serafini 2013). However, species-specific responses to fire regimes possibly depend on the availability of alternative habitats around burned areas (i.e., the regional context), an aspect that has not yet been evaluated in the *Campos Sulinos*.

Although fire has been recommended as a management tool for the conservation of grassland birds because it promotes habitat heterogeneity and diversity (Chiarani et al. 2020; Beal-Neves et al. 2020), it is worth noting that, in the *Campos Sulinos*, studies on this topic have so far been carried out only in highland grasslands, where the periodic burning of grasslands is culturally well embedded into traditional livestock management practices. Thus, the findings of these studies do not necessarily apply to the Brazilian Pampa, where fire is rarely used.

When using disturbance agents as management tools, the line between conservation and degradation can be tenuous (Zimmerman 1997; see also Andrade et al. 2023, Chap. 8 in this volume). The frequent use of fire can make the vegetation structure as simple and homogeneous as the prolonged absence of disturbances (Reinking 2005) and can also reduce habitat availability for threatened species (Isacch et al. 2004), especially when the burning period overlaps the nesting season of birds (Di Giácomo et al. 2011). Conversely, long periods without disturbance in grassland areas lead to an environmental condition that also needs restoration (Buisson et al. 2019). This is evident in some protected areas where shrub encroachment processes dominated by pioneer woody species reduce the diversity of grassland flora and fauna (Overbeck et al. 2007).

10.5 Conservation

10.5.1 Main Threats

A total of 21 level-2 IUCN threat types impact the 31 globally and/or nationally threatened and/or near-threatened species of open-vegetation ecosystems of the *Campos Sulinos* (Table 10.1; Serafini 2013; ICMBio 2018; IUCN 2021). More than half of these species are threatened by agriculture, natural system modifications and invasive species. Soybean crops, as well as eucalyptus and pine plantations, stress ecosystems across the *Campos Sulinos* via conversion and degradation (Serafini 2013; ICMBio 2018; IUCN 2021). Poorly managed livestock ranching is still frequent and leads to ecosystem degradation, indirectly affecting species, especially tallgrass specialists (Serafini 2013; ICMBio 2018; IUCN 2021). Pine tree invasion is advancing in highland and coastal grasslands, degrading grassy ecosystems (Serafini 2013; ICMBio 2018; IUCN 2021). Poor fire management in highland grasslands indirectly affects species via reduced reproductive success (Serafini 2013; ICMBio 2018; IUCN 2021). Suppression of livestock grazing or fire in protected areas leads to grassland ecosystem degradation and loss of grassland specialists (Serafini 2013; ICMBio 2018).

Herbicide and pesticide runoff from soybean crops potentially threatens 12 species (Serafini 2013; ICMBio 2018). Apart from directly stressing species via mortality, this threat may also have an indirect effect by impacting food resources (Serafini 2013; ICMBio 2018). The expansion of wind farms in highland and coastal grasslands is a new and important threat to 11 species. Wind farms convert and degrade ecosystems, stressing species directly via mortality and indirectly via disturbance (Serafini 2013; ICMBio 2018). Seven species are threatened by hunting and collecting (Serafini 2013; ICMBio 2018). *Sporophila* seedeaters are trapped more intensely in highland grasslands, whereas the Yellow Cardinal has been extirpated from a large portion of its range by this activity (Serafini 2013). Hunting for meat and feathers and persecution are important threats to the Greater Rhea and Chaco Eagle, respectively (ICMBio 2018; IUCN 2021).

10.5.2 Protected Areas

In the *Campos Sulinos*, records of threatened or near-threatened bird species of open-vegetation ecosystems have been confirmed or suspected in a total of 25 protected areas of restricted-use and sustainable-use managed by the federal or state governments (Table 10.1; Bencke et al. 2006; Serafini 2013; ICMBio 2018, 2021; eBird 2021; IAT 2021; IMA 2021; SEMA 2021; WikiAves 2021). The Black-masked Finch is currently absent from any protected area. Most of the species occur in less than five protected areas, with nine being found in a single one. Among the protected areas, the Espinilho, Guartelá, Tainhas and Vila Velha state parks have the highest number of threatened species.

Most protected areas are small and have limited grassland cover, with some not being fully implemented (Serafini 2013; ICMBio 2018; MapBiomas 2021). Tainhas State Park and the Aparados da Serra, Serra Geral and São Joaquim national parks, located in the highland grasslands, are potentially important for grassland bird conservation (Serafini 2013). Managing ecological disturbances in Brazilian protected areas is legally problematic, which limits grassland conservation (Pillar and Vélez 2010). Some protected areas where livestock grazing and fire have been suppressed appear to have lost threatened grassland birds due to shrub encroachment, such as the Aracuri-Esmeralda Ecological Station and the Ibirapuitã Biological Reserve.

Grassland remnants legally protected within private areas (i.e., Permanent Protection Areas, PPAs and Legal Reserves, LRs) are extremely important for threatened birds (Dias et al. 2013; Silva et al. 2015b; Jacoboski et al. 2017; Staude et al. 2021). However, in PPAs located within tree plantations, the suppression of grazing and, particularly, fire has led to the loss of grassland species (Dias et al. 2013; Jacoboski et al. 2017). Grassland remnants in row-crop plantations are typically found only in PPAs and in other areas where the terrain configuration hampers cultivation. PPAs may also harbor small wetlands, which are important as breeding and/or roosting sites for threatened bird species (Develey et al. 2008). PPAs located within livestock ranches often exhibit taller and denser grass compared to adjacent hillsides and hilltops, which may facilitate the conservation of both tall- and short-grass specialists at finer spatial scales (Develey et al. 2008; Jacoboski et al. 2017). The conservation value of grassland LRs in the *Campos Sulinos* has been overlooked (Overbeck et al. 2015). If well managed, livestock grazing in grassland LRs can produce economic gains for landowners and enhance bird and other biodiversity conservation (Develey et al. 2008; Overbeck et al. 2015).

10.5.3 Private Lands

Cattle ranching has been a traditional and profitable activity in the *Campos Sulinos* for centuries and provides habitat for a large proportion of the regional bird diversity (Develey et al. 2008; Vaccaro et al. 2020). This has led to a common understanding among conservationists and ranchers that cattle farming on natural pastures is an environmentally friendly land use that effectively contributes to the maintenance of grassland biodiversity (Develey et al. 2008; Bencke 2009). However, the *Campos Sulinos* have lost a third of their natural grasslands over the past 36 years through conversion to farmland and forestry (MapBiomas 2023). The existing protected areas play a minor role in conserving the remaining grassland cover of the *Campos Sulinos* (Ribeiro et al. 2021) and most of what remains is on private land. Consequently, maintenance of grassland biodiversity and ecosystem services now largely depends on privately owned land managed primarily for livestock production.

The replacement of natural grasslands by more profitable crops (mainly soybean) continues at an alarming and accelerated pace throughout the *Campos Sulinos* (MapBiomas 2023). In addition, grassland remnants are becoming increasingly concentrated in regions with shallow rocky soils not suitable for cultivation. Also, a steady shift toward more efficient land use plus inadequate management practices often cause degradation and homogenization of grassland vegetation, thus reducing the quality of natural pastures as grassland bird habitats. As a result, some rare or sensitive grassland species like large raptors and fire/grazing-intolerant tallgrass specialists are under-represented in private rangelands, while others are losing critically important habitats in regions undergoing accelerated rangeland conversion. This makes the development of policies and initiatives that encourage the maintenance of native grasslands and promote the adoption of ranching practices that enhance biological diversity on private lands all the more important and urgent.

Started in 2006, *Alianza del Pastizal* has been an example of a successful initiative that seeks to promote biodiversity conservation and sustainable livestock production in the natural grasslands of the Southern Cone of South America (https://www.alianzadelpastizal.org.br/). Led by BirdLife International through its partner organizations in Brazil, Argentina, Paraguay and Uruguay, *Alianza del Pastizal* brings together ranchers, civil organizations and local governments to promote more efficient and sustainable agricultural production systems that increase the profitability of livestock farming on rangelands while maintaining or enhancing the ecosystem services provided by native grasslands.

Through certification and labeling, *Alianza del Pastizal* provides farmers who join the initiative and commit to maintaining a minimum of 50% of native grasslands on their properties with economic and other incentives that include premium prices paid per kg at slaughter, bank credit lines at low-interest rates, technical support on best grassland management and restoration practices, private auctions of beef cattle, marketing of certified products, extension and demonstration projects, etc. In Brazil, the initiative is geographically anchored in the Brazilian Pampa (https://www.savebrasil.org.br/alianza-del-pastizal). As of May 2023, 290 landowners who together accounted for 158,000 hectares of preserved native grasslands had joined the *Alianza del Pastizal*. Since 2014, annual bird surveys using standardized methods have shown that the set of properties certified under the initiative effectively contributes to the conservation of grassland birds in the *Campos Sulinos*. As an example, 80% of the grassland bird species living in the Brazilian Pampa, including 18 species of global or regional conservation concern, have been found in a randomly selected sample of only 17 cattle ranches totaling less than 15,000 hectares (*Alianza del Pastizal* unpubl. report). Some of the major challenges faced by the initiative in Brazil include the opening of market niches that value wildlife-friendly livestock products, maintaining a production scale that meets the demands of the local beef market throughout the year, expanding the certification program to other livestock categories (e.g., calves and sheep) or products (e.g., wine, honey, leather) and increasing the competitiveness of livestock farming on natural pastures over highly profitable land uses that do not maintain grassland ecosystems (especially staple agricultural commodities like soybean) to boost long-term member loyalty and retention.

Although it is recognized that opportunities for biodiversity conservation through rangeland management on private lands are constrained by the need to maintain farm profitability and depend on the willingness of landowners to engage in conservation efforts, several ranching methods and good management practices have been identified that improve grassland bird habitat while maintaining livestock production levels. These alternatives include managing stocking rates to reduce grazing intensity, implementing rest-rotational grazing, installing temporary fences to control grazing pressure, increasing pasture size through fence removal, implementing patch burns, decreasing fire frequency, managing grasslands for vegetation heterogeneity, manipulating the location of key resources for livestock (water and supplemental feed), employing strip or patch mowing to create vegetation structural mosaics, alternating between single-species and mixed herds at different stocking rates, protecting critical habitats for breeding or resting, etc. (Bencke 2009; Askins et al. 2007; Toombs et al. 2010; Shaffer and DeLong 2019).

10.6 Research Priorities

As seen from the previous sections, a wealth of new information on the *Campos Sulinos* grassland bird species and communities has become available in the last decade alone, especially regarding habitat use and selection patterns, and reproductive biology. Also, recent analytical, theoretical and technological advances have allowed significant steps to be taken toward a better understanding of the movement ecology and evolution of grassland birds in the Neotropics. Importantly, this significant improvement in knowledge has been achieved through research carried out in a considerable part by (or with the active participation of) researchers based in the *Campos Sulinos*. This offers a promising scenario for the future of collaborative research and conservation efforts focused on grassland birds and their habitats in the region.

Notwithstanding this progress, many aspects of the ecology, natural history, conservation, and evolution of grassland birds have not been investigated at all or remain poorly understood in the *Campos Sulinos*. For example, despite being important stressors for grassland birds and their habitats (Jarzyna et al. 2016), threats related to climate change have been largely neglected in the *Campos Sulinos*. Another significant knowledge gap relates to the effects of agrochemicals on grassland bird populations and their food resources. The lack of adequate information on diet and foraging ecology prevents us from assessing how much grassland birds depend on specific food resources or contribute to the control of potential agricultural pests. Regarding habitat use and selection, we still know very little about how the probability of occurrence and density of grassland bird species vary with the size and spatial configuration of habitat patches in different timescales (Ribic et al. 2009), particularly in grassland landscapes highly fragmented by cropland agriculture. Climatic and edaphic factors may affect the abundance of some species (Davis et al. 2021), but there is no information on the effects of annual variations in precipitation and soil moisture on the abundance of grassland birds. Similarly, the responses of grassland bird species and communities to different restoration interventions are still poorly investigated, even though the ecological restoration of grasslands has become a priority in view of the increasing levels of degradation observed in the *Campos Sulinos*. With regard to conservation initiatives on private lands, understanding how and to what extent recommended best practices aimed at improving grassland bird habitats interfere with the profitability of farms, and how effective they are for birds, is an important conservation issue. Last, but not least, the gaps in our knowledge of the natural history of most grassland bird species in the *Campos Sulinos* need to be filled if we want to better understand the processes that regulate their populations and define more effective conservation strategies for their conservation, despite the scarce resources available for scientific research in Brazil and the difficulties involved in publishing natural history studies in high-impact journals. Table 10.2, while admittedly incomplete, lists research priorities based on information gaps identified in this review and is intended to serve as an agenda to help direct research efforts to improve our knowledge of the grassland birds of the *Campos Sulinos*, with a view to contributing to their conservation.

Table 10.2 Key research priorities for advancing knowledge on open-vegetation birds in the *Campos Sulinos*, grouped by topics

Diversity and composition
Conduct evaluations of alpha and beta diversity patterns, considering taxonomic, functional and phylogenetic aspects, and their underlying processes
Develop a trait-based classification system for grassland birds to assess their level of habitat specialization
Investigate the historical biogeography of bird species in the *Campos Sulinos*
Quantify the population sizes of threatened species in the *Campos Sulinos* to identify conservation priority areas
Ecology and natural history
Evaluate the impact of habitat structure on community-level functional and phylogenetic diversity
Investigate the relationship between habitat structure and organism-level diversity across different life stages and spatial scales
Uncover hidden migratory species and identify migration patterns
Determine the geographical connectivity between breeding and wintering grounds, migration routes and critical stopover sites
Assess carry-over effects, connectivity and migratory networks
Study the breeding biology of a wider range of grassland birds, particularly *Anthus* spp., paleognaths, raptors and swallows
Evaluate breeding success and nest predation using non-invasive techniques such as video cameras and camera traps
Increase studies on the trophic ecology of open-vegetation birds
Effects of land use patterns on avian communities
Evaluate the effects of agrochemicals and agricultural expansion on threatened species, community-level functional and phylogenetic diversity, and the viability of grassland species within tree plantations

(continued)

Table 10.2 (continued)

Assess the impacts of pine tree cultivation and invasion on adjacent grassland remnants in highland grasslands, as well as the ecological consequences of frequent fire use on vegetation structure and habitat availability for threatened species
Examine the effects of grassland restoration in former tree plantations and livestock ranching on community-level functional and phylogenetic diversity
Establish manipulative experiments to evaluate the effect of different stocking rates on avian diversity and reproduction in natural grasslands, considering the availability of alternative habitats around burned areas and species-specific responses to fire regimes
Conduct long-term studies to understand the cumulative effects, recovery trajectories, and the delicate balance between disturbance and restoration in ecosystem management after fires
Conservation
Assess the effects of climate change on avian diversity, reproduction and the population viability of threatened species within protected areas
Investigate how the characteristics (area, shape, spatial configuration, isolation) of grassland patches within and around protected areas influence the occurrence of threatened birds and evaluate the effectiveness of the protected areas system in conserving them
Conduct surveys within protected areas to confirm the occurrence of threatened species and identify additional ones
Assess the impacts of grazing, fire suppression and management practices within protected areas on threatened birds
Evaluate the role of private reserves, permanent protection areas and grassland legal reserves in conserving threatened grassland birds
Expand the protected areas system in grasslands, focusing on wildlife refuge categories that enable the coexistence of livestock and threatened birds
Assess the impact of invasive species, particularly the South African grass *Eragrostis plana*, on threatened birds

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Appendix

Grassland birds of the *Campos Sulinos*, southern Brazil, with selected ecological, physical, behavioral and distributional traits.

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Rheidae										
Rhea americana (Linnaeus, 1758)	Greater Rhea	F	2	X	Y	–	N	Br Res	–	7
Tinamidae										
Crypturellus parvirostris (Wagler, 1827)	Small-billed Tinamou	F	–	–	Y	–	N	Br Res	–	7
Rhynchotus rufescens (Temminck, 1815)	Red-winged Tinamou	O	2	X	Y	–	N	Br Res	–	7
Nothura maculosa (Temminck, 1815)	Spotted Nothura	O	2	X	Y	–	N	Br Res	–	7
Taoniscus nanus (Temminck, 1815)	Dwarf Tinamou	O	–	X	Y	–	–	Ext	–	10
Anatidae										
Chloephaga picta (Gmelin, 1789)	Upland Goose	F	2	X	–	–	–	Vag	Cool-temp	–
Columbidae										
Patagioenas picazuro (Temminck, 1813)	Picazuro Pigeon	F	–	X	N	–	Y	Br Res	–	7
Zenaida auriculata (Des Murs, 1847)	Eared Dove	F	–	–	(Y)	–	Y	Br Res	–	4
Caprimulgidae										
Hydropsalis anomala (Gould, 1838)	Sickle-winged Nightjar	–	2	–	N	–	Y	Br Res	–	16
Hydropsalis longirostris (Bonaparte, 1825)	Band-winged Nightjar	O	3	–	(Y)	–	?	Br Res	–	3
Hydropsalis torquata (Gmelin, 1789)	Scissor-tailed Nightjar	F	–	X	Y	–	?	Br Res	–	7

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Nannochordeiles pusillus (Gould, 1861)	Least Nighthawk	O	–	X	Y	–	?	Br Res	–	5
Podager nacunda (Vieillot, 1817)	Nacunda Nighthawk	F	2	X	Y	–	?	Br Migr	Temp-trop	3
Trochilidae										
Polytmus guainumbi (Pallas, 1764)	White-tailed Goldenthroat	O	3	X	N	–	N	Br Res	–	5
Rallidae										
Micropygia schomburgkii (Schomburgk, 1848)	Ocellated Crake	–	–	X	Y	–	N	Br Res?	–	5
Charadriidae										
Pluvialis dominica (Statius Muller, 1776)	American Golden-Plover	(O)	2	–	–	–	N	NBr Migr	Near-Neot	24
Oreopholus ruficollis (Wagler, 1829)	Tawny-throated Dotterel	O	2	X	–	–	N	NBr Migr	Cool-temp	6
Vanellus chilensis (Molina, 1782)	Southern Lapwing	O	2	X	Y	–	Y	Br Res	–	3
Charadrius modestus Lichtenstein, 1823	Rufous-chested Dotterel	O	2	X	–	–	N	NBr Migr	Cool-temp	6
Scolopacidae										
Bartramia longicauda (Bechstein, 1812)	Upland Sandpiper	O	2	–	–	–	N	NBr Migr	Near-Neot	24
Calidris subruficollis (Vieillot, 1819)	Buff-breasted Sandpiper	O	2	–	–	–	N	NBr Migr	Near-Neot	24
Gallinago undulata (Boddaert, 1783)	Giant Snipe	O	–	X	Y	–	Y	Br Res	–	5
Gallinago paraguaiae (Vieillot, 1816)	South American Snipe	O	–	–	Y	–	Y	Br Res	–	3

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Thinocoridae										
Thinocorus rumicivorus Eschscholtz, 1829	Least Seedsnipe	F	2	X	–	–	–	Vag	Cool-temp	–
Ardeidae										
Bubulcus ibis (Linnaeus, 1758)	Cattle Egret	F	2	X	N	–	N	Br Res	–	0
Syrigma sibilatrix (Temminck, 1824)	Whistling Heron	F	–	X	N	–	N	Br Res	–	3
Threskiornithidae										
Theristicus caerulescens (Vieillot, 1817)	Plumbeous Ibis	F	–	X	N	–	N	Br Res	–	18
Theristicus caudatus (Boddaert, 1783)	Buff-necked Ibis	F	2	X	N	–	N	Br Res	–	3
Cathartidae										
Cathartes aura (Linnaeus, 1758)	Turkey Vulture	F	–	X	N	–	N	Br Res	–	1
Cathartes burrovianus Cassin, 1845	Lesser Yellow-headed Vulture	F	–	X	N	–	N	Br Res	–	2
Accipitridae										
Gampsonyx swainsonii Vigors, 1825	Pearl Kite	F	–	X	N	–	N	Br Res	–	4
Elanus leucurus (Vieillot, 1818)	White-tailed Kite	F	3	X	N	–	N	Br Res	–	1
Circus cinereus Vieillot, 1816	Cinereous Harrier	F	2	X	(Y)	–	Y	Br Res	–	6
Heterospizias meridionalis (Latham, 1790)	Savanna Hawk	F	3	X	N	–	N	Br Res	–	4
Urubitinga coronata (Vieillot, 1817)	Crowned Eagle	F	3	–	N	–	N	Br Res	–	13
Geranoaetus albicaudatus (Vieillot, 1816)	White-tailed Hawk	F	2	X	N	–	N	Br Res	–	2
Geranoaetus melanoleucus (Vieillot, 1819)	Black-chested Buzzard-Eagle	F	2	X	N	–	N	Br Res	–	3

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Buteo swainsoni Bonaparte, 1838	Swainson's Hawk	O	2	–	–	–	N	NBr Migr	Near-Neot	24
Strigidae										
Athene cunicularia (Molina, 1782)	Burrowing Owl	O	2	X	Y	–	N	Br Res	–	1
Asio flammeus (Pontoppidan, 1763)	Short-eared Owl	O	2	X	Y	–	Y	Br Res	–	0
Picidae										
Colaptes campestris (Vieillot, 1818)	Campo Flicker	F	3	X	N	–	N	Br Res	–	9
Cariamidae										
Cariama cristata (Linnaeus, 1766)	Red-legged Seriema	F	2	X	N	–	N	Br Res	–	9
Falconidae										
Caracara plancus (Miller, 1777)	Crested Caracara	F	2	X	N	–	N	Br Res	–	2
Milvago chimango (Vieillot, 1816)	Chimango Caracara	F	2	X	(Y)	–	N	Br Res	–	6
Falco sparverius Linnaeus, 1758	American Kestrel	(F)	3	X	N	–	N	Br Res	–	1
Falco femoralis Temminck, 1822	Aplomado Falcon	O	2	X	N	–	N	Br Res	–	1
Psittacidae										
Myiopsitta monachus (Boddaert, 1783)	Monk Parakeet	F	–	–	N	–	N	Br Res	–	17
Scleruridae										
Geositta cunicularia (Vieillot, 1816)	Common Miner	O	2	X	Y	N	N	Br Res	–	6
Furnariidae										
Furnarius rufus (Gmelin, 1788)	Rufous Hornero	F	3	–	N	N	N	Br Res	–	8
Cinclodes pabsti Sick, 1969	Long-tailed Cinclodes	F	1	X	Y	N	N	Br Res	–	23
Cinclodes fuscus (Vieillot, 1818)	Buff-winged Cinclodes	F	3	X	–	N	N	NBr Migr	Cool-temp	6
Phacellodomus striaticollis (d'Orbigny & Lafresnaye, 1838)	Freckle-breasted Thornbird	–	3	–	N	N	N	Br Res	–	19

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Anumbius annumbi (Vieillot, 1817)	Firewood-Gatherer	F	–	X	N	Y	N	Br Res	–	17
Asthenes hudsoni (Sclater, 1874)	Hudson's Canastero	F	2	X	Y	Y	N	Br Res	–	20
Asthenes pyrrholeuca (Vieillot, 1817)	Sharp-billed Canastero	F	–	X	–	–	–	Vag	Cool-temp	–
Spartonoica maluroides (d'Orbigny & Lafresnaye, 1837)	Bay-capped Wren-Spinetail	–	2	–	N	Y	N	Br Res	–	22
Schoeniophylax phryganophilus (Vieillot, 1817)	Chotoy Spinetail	–	–	X	N	Y	N	Br Res	–	12
Synallaxis albescens Temminck, 1823	Pale-breasted Spinetail	F	–	X	N	N	N	Br Res	–	2
Tyrannidae										
Elaenia chiriquensis Lawrence, 1865	Lesser Elaenia	F	–	X	N	N	N	Br Migr	Intra-trop	4
Culicivora caudacuta (Vieillot, 1818)	Sharp-tailed Tyrant	O	2	X	N	Y	N	Br Res	–	5
Polystictus pectoralis (Vieillot, 1817)	Bearded Tachuri	O	1	X	N	N	Y	Br Res	–	5
Machetornis rixosa (Vieillot, 1819)	Cattle Tyrant	F	3	–	N	N	N	Br Res	–	3
Tyrannus savana Daudin, 1802	Southern Fork-tailed Flycatcher	O	3	X	N	N	Y	Br Migr	Temp-trop	2
Pyrocephalus rubinus (Boddaert, 1783)	Vermilion Flycatcher	–	–	X	N	Y/N	Y	Br Migr	Temp-trop	1
Gubernetes yetapa (Vieillot, 1818)	Streamer-tailed Tyrant	F	2	X	N	N	N	Br Res	–	10
Heteroxolmis dominicana (Vieillot, 1823)	Black-and-white Monjita	F	2	X	N	N	N	Br Res	–	21
Alectrurus tricolor (Vieillot, 1816)	Cock-tailed Tyrant	O	1	X	Y?	N	Y	Br Res	–	10

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Alectrurus risora (Vieillot, 1824)	Strange-tailed Tyrant	F	2	X	–	–	–	Vag	–	–
Muscisaxicola maclovianus (Garnot, 1826)	Dark-faced Ground-Tyrant	F	–	X	–	–	–	Vag	Cool-temp	–
Muscisaxicola capistratus (Garnot, 1826)	Cinnamon-bellied Ground-Tyrant	F	–	X	–	–	–	Vag	Cool-temp	–
Lessonia rufa (Gmelin, 1789)	Austral Negrito	F	2	–	–	N	N	NBr Migr	Cool-temp	6
Knipolegus lophotes Boie, 1828	Crested Black-Tyrant	–	2	–	N	N	N	Br Res	–	14
Xolmis irupero (Vieillot, 1823)	White Monjita	F	3	–	N	N	?	Br Res	–	3
Xolmis velatus (Lichtenstein, 1823)	White-rumped Monjita	F	–	–	N	N	?	Br Res	–	10
Nengetus cinereus (Vieillot, 1816)	Gray Monjita	F	2	X	N	N	Y	Br Res	–	11
Nengetus coronatus (Vieillot, 1823)	Black-crowned Monjita	F	–	–	–	N	N	NBr Migr	Cool-temp	6
Nengetus rubetra (Burmeister, 1860)	Rusty-backed Monjita	F	–	–	–	–	–	Vag	Cool-temp	–
Nengetus rufiventris (Vieillot, 1823)	Chocolate-vented Tyrant	F	2	X	–	–	–	Vag	Cool-temp	–
Agriornis micropterus Gould, 1839	Gray-bellied Shrike-tyrant	F	–	–	–	–	–	Vag	Cool-temp	–
Agriornis murinus (d'Orbigny & Lafresnaye, 1837)	Lesser Shrike-tyrant	F	–	–	–	–	–	Vag	Cool-temp	–
Hirundinidae										
Alopochelidon fucata (Temminck, 1822)	Tawny-headed Swallow	–	2	X	Y	N	N	Br Res	–	3
Progne tapera (Linnaeus, 1766)	Brown-chested Martin	–	2	X	N	N	Y	Br Migr	Temp-trop	2

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Tachycineta leucorrhoa (Vieillot, 1817)	White-rumped Swallow	–	3	X	N	N	N	Br Res	–	3
Tachycineta leucopyga (Meyen, 1834)	Chilean Swallow	–	3	X	–	N	N	NBr Migr	Cool-temp	6
Hirundo rustica Linnaeus, 1758	Barn Swallow	–	3	X	–	N	N	NBr Migr	Near-Neot	0
Petrochelidon pyrrhonota (Vieillot, 1817)	Cliff Swallow	–	3	X	–	N	N	NBr Migr	Near-Neot	24
Troglodytidae										
Cistothorus platensis (Latham, 1790)	Grass Wren	O	2	X	N	Y	N	Br Res	–	2
Mimidae										
Mimus saturninus (Lichtenstein, 1823)	Chalk-browed Mockingbird	–	3	X	N	N	Y	Br Res	–	3
Motacillidae										
Anthus chii Vieillot, 1818	Yellowish Pipit	O	2	X	Y	Y	Y	Br Res	–	3
Anthus furcatus d'Orbigny & Lafresnaye, 1837	Short-billed Pipit	O	2	X	Y	Y	Y	Br Res	–	6
Anthus correndera Vieillot, 1818	Correndera Pipit	O	2	X	Y	Y	Y	Br Res	–	6
Anthus nattereri Sclater, 1878	Ochre-breasted Pipit	O	1	X	Y	Y	Y	Br Res	–	15
Anthus hellmayri Hartert, 1909	Hellmayr's Pipit	O	1	X	Y	Y	Y	Br Res	–	6
Passerellidae										
Ammodramus humeralis (Bosc, 1792)	Grassland Sparrow	O	2	X	Y	Y	N	Br Res	–	3
Zonotrichia capensis (Statius Muller, 1776)	Rufous-collared Sparrow	F	–	X	(Y)	Y	N	Br Res	–	2
Icteridae										
Dolichonyx oryzivorus (Linnaeus, 1758)	Bobolink	O	3	–	–	Y/N	N	Tran	Near-Neot	24

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Leistes superciliaris (Bonaparte, 1850)	White-browed Meadowlark	O	2	X	Y	Y/N	Y	Br Res	–	3
Leistes defilippii (Bonaparte, 1850)	Pampas Meadowlark	O	1	X	–	–	–	Ext	–	20
Molothrus rufoaxillaris Cassin, 1866	Screaming Cowbird	F	3	–	N	N	N	Br Res	–	6
Molothrus bonariensis (Gmelin, 1789)	Shiny Cowbird	F	3	–	N	N	Y	Br Res	–	2
Gnorimopsar chopi (Vieillot, 1819)	Chopi Blackbird	F	–	X	N	N	N	Br Res	–	3
Agelaioides badius (Vieillot, 1819)	Grayish Baywing	F	–	–	N	N	N	Br Res	–	6
Xanthopsar flavus (Gmelin, 1788)	Saffron-cowled Blackbird	O	2	X	N	N	N	Br Res	–	21
Pseudoleistes guirahuro (Vieillot, 1819)	Yellow-rumped Marshbird	O	2	X	N	N	N	Br Res	–	15
Pseudoleistes virescens (Vieillot, 1819)	Brown-and-yellow Marshbird	F	2	–	N	N	N	Br Res	–	21
Thraupidae										
Coryphaspiza melanotis (Temminck, 1822)	Black-masked Finch	O	2	X	?	Y	N	Br Res?	–	10
Embernagra platensis (Gmelin, 1789)	Great Pampa-Finch	O	2	X	Y	Y/N	N	Br Res	–	6
Emberizoides herbicola (Vieillot, 1817)	Wedge-tailed Grass-Finch	O	2	X	Y	Y	Y	Br Res	–	5
Emberizoides ypiranganus Ihering & Ihering, 1907	Lesser Grass-Finch	O	2	X	Y	Y	Y	Br Res	–	15
Saltatricula multicolor (Burmeister, 1860)	Many-colored Chaco Finch	F	–	–	–	–	–	Vag	–	–

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Volatinia jacarina (Linnaeus, 1766)	Blue-black Grassquit	F	2	X	N	Y/N	Y	Br Res	–	2
Sporophila lineola (Linnaeus, 1758)	Lined Seedeater	F	–	X	N	N	N	Br Migr	Temp-trop	7
Sporophila plumbea (Wied, 1830)	Plumbeous Seedeater	O	–	–	N	N	N	Br Migr	Intra-trop	5
Sporophila beltoni Repenning & Fontana, 2013	Tropeiro Seedeater	O	1	X	N	N	N	Br Migr	Temp-trop	23
Sporophila nigricollis (Vieillot, 1823)	Yellow-bellied Seedeater	F	–	X	N	N	N	Br Res?	–	5
Sporophila caerulescens (Vieillot, 1823)	Double-collared Seedeater	F	–	X	N	N	N	Br Res	–	3
Sporophila leucoptera (Vieillot, 1817)	White-bellied Seedeater	F	–	X	N	N	N	Br Res	–	7
Sporophila pileata (Sclater, 1865)	Pearly-bellied Seedeater	O	2	X	N	N	N	Br Migr	Temp-trop	16
Sporophila hypoxantha Cabanis, 1851	Tawny-bellied Seedeater	O	2	X	N	N	N	Br Migr	Temp-trop	15
Sporophila ruficollis Cabanis, 1851	Dark-throated Seedeater	O	2	X	N	N	N	Br Migr	Temp-trop	20
Sporophila palustris (Barrows, 1883)	Marsh Seedeater	O	2	X	N	N	N	Br Migr	Temp-trop	20
Sporophila hypochroma Todd, 1915	Rufous-rumped Seedeater	O	2	X	N	N	N	Br Migr?	Temp-trop	20
Sporophila cinnamomea (Lafresnaye, 1839)	Chestnut Seedeater	O	2	X	N	N	N	Br Migr	Temp-trop	20
Sporophila melanogaster (Pelzeln, 1870)	Black-bellied Seedeater	O	2	X	N	N	N	Br Migr	Temp-trop	23

Family/Scientific name	Common name	O/F[a]	Azp[b]	Par[c]	GrNest[d]	StrPlum[e]	AeDisp[f]	Stat[g]	Migr[h]	Dist[i]
Donacospiza albifrons (Vieillot, 1817)	Long-tailed Reed Finch	F	2	X	N	Y	Y	Br Res	–	15
Sicalis citrina Pelzeln, 1870	Stripe-tailed Yellow-Finch	F	2	X	(Y)	Y/N	N	Br Res	–	5
Sicalis luteola (Sparrman, 1789)	Grassland Yellow-Finch	O	2	X	Y	Y/N	Y	Br Res	–	3

[a] Obligate/facultative grassland specialist (sensu Vickery et al. 1999): O – obligate, F – facultative (in parentheses if O/F in North America only)
[b] Grassland-use category in southeastern South America (Azpiroz et al. 2012): 1 – species restricted to grassland habitats (i.e., do not use alternative habitats), 2 – species that make extensive use of grassland habitats, but also use other habitats, 3 – species that make extensive use of grassland habitats only in certain regions
[c] Species that have some type of grassland as their primary habitat in the Neotropics (habitat codes N5, N6, N7, N13 and N14 of Parker et al. 1996)
[d] Ground nesting: Y – yes (in parentheses, if facultative), N – no
[e] Contrastingly striped plumage (passerines only): Y – yes, N – no, Y/N – only in one sex or age class
[f] Aerial display: Y – yes, N – no
[g] Occurrence status (in the *Campos Sulinos*): Br Res – breeding resident, Br Migr – breeding migrant, NBr Migr – non-breeding migrant, Tran – transient migrant, Vag – vagrant, Ext – extinct
[h] Migration system: Near-Neot – Nearctic-Neotropical migrant, Temp-trop – Neotropical austral/temperate-tropical migrant, Cool-temp – Neotropical austral/cool-temperate migrant, Intra-trop – Intra-tropical migrant (see text)
[i] Distribution center: 0 – Cosmopolitan, 1 – Open areas throughout Americas, 2 – Open areas of South and Central America, 3 – Open areas of South America, 4 – Open areas of tropical South and Central America, 5 – Open areas of tropical South America, 6 – Open areas of temperate South America, 7 – Dry diagonal (Luebert 2021), 8 – Dry diagonal+Pampa, 9 – Dry diagonal+highland grasslands, 10 – Cerrado, 11 – Cerrado+Chaco+Pampa+Espinal+*Campos Sulinos*, 12 – Cerrado+Chaco+Pampa+Espinal, 13 – Cerrado+Chaco+Espinal+highland grasslands, 14 – Cerrado+highland grasslands+Uruguayan savanna, 15 – Cerrado+*Campos Sulinos*+Pampa, 16 – Cerrado+*Campos Sulinos*, 17 – Chaco+Espinal+Pampa+highland grasslands, 18 – Chaco+Espinal+Pampa, 19 – Pampa+Espinal+Campos Sulinos, 20 – *Río de la Plata* grasslands, 21 – Pampa+*Campos Sulinos*, 22 – Pampa+Espinal, 23 – Highland grasslands, 24 – Open areas of North America

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Chapter 11
Mammals of the *Campos Sulinos*: Diversity and Conservation

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11.1 Introduction

Brazil is a megadiverse country and home to over 750 species of mammals (Paglia et al. 2012; Quintela et al. 2020). Among the many environments contributing to its unique biodiversity, the Southern Brazilian grasslands – hereafter '*Campos Sulinos*' – stand out for their high species-area relationship. The *Campos Sulinos* occupy only ~3% of the Brazilian territory (~222,137 km^2) and comprise grassy landscapes from two different Brazilian biomes, the Pampa and the Atlantic Forest (Vélez-Martin et al. 2015). Despite this relatively small area, ~18% of the Brazilian mammals occur in the region (Gonçalves et al. 2014; Luza et al. 2015).

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The *Campos Sulinos* is a biogeographic ecotone where populations of different species from tropical and temperate habitats meet (Queirolo 2016). This confluence of biotic zones gives rise to unique ecological and evolutionary patterns, such as hybridization zones (Trigo et al. 2008) and key adaptations to persist in a highly heterogeneous and dynamic landscape (Luza et al. 2015, 2016). The *Campos Sulinos* represent the distribution limit of many species and, as such, can be expected to contain marginal populations with high genetic and morphological variability (Sexton et al. 2009), an appropriate scenario for high speciation rates and for the emergence of evolutionary novelties. These processes are compatible with the steep species-area relationship found for the *Campos Sulinos* mammals, and with the occurrence of interesting ecological adaptations. Nonetheless, a quarter of the mammal species are threatened with extinction due to rapid habitat loss, illegal hunting, and introduction of invasive species, which are all accentuated by the small area under integrally protected reserves (de Freitas et al. 2009; Lima et al. 2018, 2020). Despite this diversity and level of threat, knowledge on the *Campos Sulinos* mammals is still incipient (Prevedello et al. 2008).

To provide a spatial and topical contextualization of research efforts and propose advances in current scientific knowledge, we assembled a dataset comprising bibliographic (composition of authors, publication year, journal, title, abstract, DOI), geographic (latitude-longitude coordinates) and taxonomic information from published sources on the mammals of the *Campos Sulinos*. This dataset was assembled using two data sources: (1) Web of Science collection (Clarivate Analytics 2021, https://clarivate.com) and (2) researchers' knowledge. In Web of Science, peer-reviewed papers were searched on 20 December 2021, using the following sequence of terms: "mammal*" AND "grassland*" AND "south* Brazil" NOT "southeastern" NOT "southwestern" NOT "cerrado". Researchers' knowledge consisted of studies known by the authors and chapter reviewers. Data from both sources were then combined, yielding a pool of 92 studies conducted in the *Campos Sulinos* since 1982.

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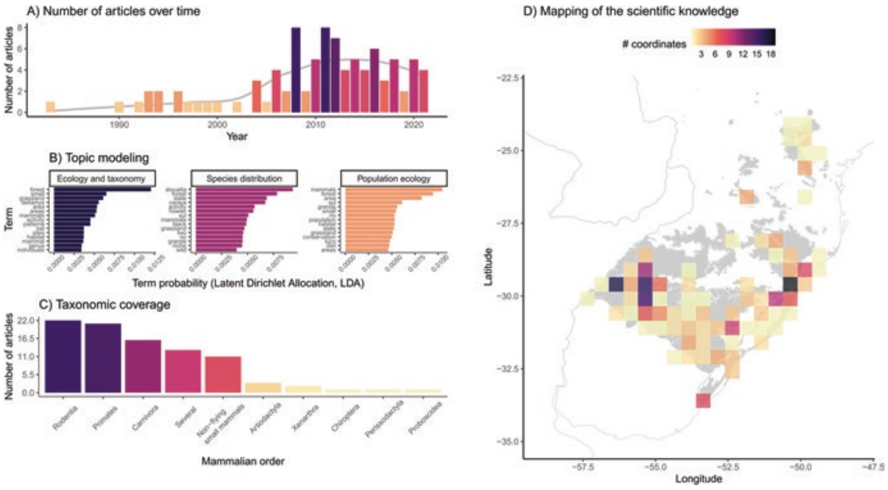

Fig. 11.1 Trends in publication over time (**a**), the most frequent topics (**b**), taxonomic coverage (**c**), and spatial distribution of mammalian research in the *Campos Sulinos* (**d**). Knowledge spatialization (**d**) was based on 273 coordinates from 92 articles. All data, codes and results can be found in the GitHub of André L. Luza (see Data Availability Statement). Cell size: 0.5° lat-long degrees (ca. 55 × 55 km)

Although research on the *Campos Sulinos* mammals began in the 1980s and expanded in the 1990s (Ximenez 1982; de Freitas et al. 1983; Bicca-Marques 1990; Bicca-Marques and Calegaro-Marques 1994, among others), the peak in the number of studies only occurred almost 30 years later, in 2008 and 2011, with eight articles published each year (Fig. 11.1a). The scientific information contained in the 92 articles was synthesized using a topic modeling analysis (Griffiths and Steyvers 2004; Cao et al. 2009), applied to individualized (or 'tokenized') words extracted from article titles and abstracts. Using this analysis, we found that most mammalian research in the *Campos Sulinos* focused on three main topics (Fig. 11.1b). The most frequent topic, with the highest number of articles, was "Species distribution", followed by "Population ecology" and "Ecology and taxonomy".

The topic "Species distribution" comprised mainly studies on mammal distribution and habits, with a high representativeness of studies on the southernmost distribution limits of the black-and-gold howler monkey (*Alouatta caraya*) (e.g., Bicca-Marques 1990; Bicca-Marques et al. 2008; Jardim et al. 2020), greater naked-tailed armadillo (*Cabassous tatouay*, Oliveira et al. 2015), and small big-eared brown bat (*Histiotus montanus*, Miranda et al. 2008). The topic "Population ecology" predominantly included studies on species feedings habits (e.g., Tomazzoni et al. 2005; Prates and Bicca-Marques 2008; Silva-Pereira et al. 2011; Kasper et al. 2016), demography (e.g., Braga and Kuniyoski 2010; Kasper et al. 2012), genetic diversity and conservation genetics (e.g., Medeiros et al. 2020). The topic "Ecology and taxonomy" included a varied set of articles on habitat use and daily activity of rodents and marsupials (e.g., Lima et al. 2010; Kasper et al. 2012; Luza et al. 2016), wild cats (e.g., Tirelli et al. 2018), and primates (e.g., Bicca-Marques and Calegaro-Marques 1998), bats (e.g., Barros et al. 2014), and on the taxonomy and systematics of rodents (e.g., Ventura et al. 2011; de Freitas et al. 1983, 2012; Christoff et al. 2016). Further exploration of the dataset regarding the distribution of articles among mammalian orders showed that rodents, primates and carnivorans were the most studied groups. Extinct taxa were also studied (some Xenarthra, Proboscidea) (Asevedo et al. 2020; Lopes et al. 2021) (Fig. 11.1c). Conservation and other relevant and current topics such as ecosystem functioning and ecosystem services did not emerge as topics having a cohesive body of literature, a gap that we explore below (Sect. 11.4).

We also explored the spatial coverage of scientific research in the *Campos Sulinos*. To accomplish this, the region was divided into a grid of 78 half-degree cells (ca. 55 km^2 each). We then superimposed the 273 site coordinates extracted from the 92 articles. A total of 49 (63%) out of the 78 cells had at least one study about mammals, the majority concentrated in the state of Rio Grande do Sul (RS), where most of the *Campos Sulinos* area is located (RS; Fig. 11.1d). Two main research hotspots (i.e., areas of high research concentration) were identified in RS: in the western (municipalities of Alegrete and Santana do Livramento) and northeastern portions of the state (municipalities of São Francisco de Paula and Cambará do Sul) (Fig. 11.1d). A broad range of research was conducted in these regions, with a focus on Carnivora and Primates in the west (e.g., Bicca-Marques 1990; Tirelli et al. 2018), and on the orders Rodentia and Didelphimorphia in the northeast and coastal plain (e.g., Pedó et al. 2010; Quintela et al. 2014a, b).

Nonetheless, both the *Planalto das Missões* in northwestern RS, known to host the last remnants of *Aristida jubata* grasslands in the state (Overbeck et al. 2015), and the highland grasslands of Santa Catarina and Paraná are large areas (comprising together ~1600 km^2) with virtually no scientific research (Fig. 11.1c). These regions should be regarded as priorities for studies on mammals, particularly to tackle the Linnean and Wallacean shortfalls (i.e., knowledge gaps on taxonomy and distribution; Bini et al. 2006). New species descriptions (e.g., the rodents *Scapteromys meridionalis* and *Deltamys araucaria* [Quintela et al. 2014a, 2017], bat *Myotis pampa* [Novaes et al. 2021], and felid *Leopardus munoai* [Nascimento et al. 2021]), and novel distributional records from understudied groups (e.g., the rodents *Oxymycterus judex* [Luza et al. 2015; Peçanha et al. 2020], *Castoria angustidens* [formely *Akodon serrensis*, Luza et al. 2015], and *Calomys tener* [Quintela et al. 2014b; Salazar-Bravo 2015]) are likely to be produced from these under-sampled areas in the near future. As seen, both the spatialization of existing scientific knowledge and the identification of important information gaps encourage an expansion of mammalian research in the *Campos Sulinos* in order to increase the spatial coverage of research and improve the number of study topics.

In the remainder of this chapter, the state-of-the-art knowledge on the mammals of the *Campos Sulinos* is described and discussed, with a focus on relevant issues and knowledge gaps regarding taxonomy, distribution, ecology, and evolution. We present the composition and distribution of mammals inhabiting the *Campos Sulinos* grasslands (Sect. 11.2), the factors potentially promoting speciation and hybridization in this region (11.3), and the adaptations shown by mammals to thrive in these grassy landscapes (11.4). Then, we discuss the ecosystem services provided by mammals while addressing their conservation needs (11.5). This chapter ends by identifying topics that researchers, government, landowners, and society should consider to improve research and public policy decisions in health, nature conservation, and sustainable use of natural resources (11.6).

11.2 Which Mammals Live in the *Campos Sulinos*?

The compilation of the mammalian diversity in the *Campos Sulinos* resulted in a list of 134 species (Table 11.1), 11 of which (8%) are endemic. Rodents and bats are the most speciose groups, which is expected given their predominance among the Neotropical mammals (Paglia et al. 2012; Patton et al. 2015). Carnivores and ungulates are the most representative orders in the *Campos Sulinos* (Jardim 2007).

Carnivora is represented by 18 species belonging to families Canidae, Felidae, Mephitidae, Mustelidae, and Procyonidae (species list in Kasper et al. 2014 and Queirolo 2016). While most carnivore species are widely distributed, many populations currently exhibit significant declines or are already extinct in the region. For example, the maned wolf (*Chrysocyon brachyurus*), although originally distributed from the Cerrado and Pantanal in central Brazil to northeastern Argentina and Rio Grande do Sul, is now very rare in the *Campos Sulinos* (Paula and DeMatteo 2015). The situation of the jaguar (*Panthera onca*) is equally worrisome. The species is distributed from the southern USA to southern Brazil but is 'Regionally Extinct' in the Pampa and probably throughout the *Campos Sulinos*. The *Campos Sulinos* also are home to narrow-ranging species, such as the recently revalidated Muñoa's Pampas cat (*Leopardus munoai*) (Nascimento et al. 2021). This small cat is endemic to the Uruguayan Savanna ecoregion (Nascimento et al. 2021; Tirelli et al. 2021), which includes the southern part of the *Campos Sulinos*. There are also taxonomic uncertainties on the status of some taxa found in the region (e.g., *Conepatus chinga*, Kasper et al. 2009).

Chiroptera is represented in the *Campos Sulinos* by at least 34 species belonging to three families: Phyllostomidae, Vespertilionidae, and Molossidae (species list in de Freitas and Quintela 2014 and da Costa and Ramos Pereira 2022). The Phyllostomidae occurring in the *Campos Sulinos* include frugivore, nectarivore/insectivore, carnivore, and sanguinivore species, while Vespertilionidae and Molossidae are exclusively insectivores. Most species found in the *Campos Sulinos* are widely distributed in the Neotropics, although some are more restricted to southern Brazil, such as the Patagonian dwarf bonneted bat *Eumops patagonicus*.

The order Chiroptera, however, presents significant Linnean and Wallacean shortfalls throughout the Brazilian territory (Bernard et al. 2011; Aguiar et al. 2021), including the *Campos Sulinos*. Grassy landscapes pose challenges for surveying bats using more standardized/classic sampling techniques, such as mist-nests, which are easily detected and avoided by these animals in open habitats. The growing use

Table 11.1 Synthesis of major mammalian taxa of the *Campos Sulinos*, showing their species richness, conservation status, and occurrence in the Pampa and Atlantic Forest

Superorder/ Order	N Families	N Species	N endemics	N species regionally threatened or DD (FZB, 2014)	Regionally extinct	Pampa & Atlantic Forest	Only Pampa	Only Atlantic Forest
Carnivora	5	18	2[a]	12	2[b]	16	2	0
Chiroptera	5	36	1[c]	2	0	33	1	2
Didelphimorphia	1	15	0	5	0	14	1	0
Lagomorpha	1	1	0	1	0	1	0	0
Primates	2	4	0	3[d]	0	0	1	3
Rodentia	7	48	8	7	0	28	12	8
Ungulata	2	6	0	5	0	2	1	3
Xenarthra	2	6	0	4	0	6	0	0

The Superorder Ungulata includes the orders Artiodactyla and Perissodactyla, and the Superorder Xenarthra includes the orders Cingulata and Pilosa

[a] Includes a species of small wild cat, the Muñoa's Pampas cat (*Leopardus munoai*) (Nascimento et al. 2021; Tirelli et al. 2021), threatened with extinction (Tirelli et al. 2021); in addition, although still under debate, the population of *Conepatus chinga* that occurs in southern Brazil and Uruguay may be a distinct species given its genetic and morphological distinctiveness and geographical isolation; if confirmed, it will be another endemic carnivoran in the region (Rodrigues 2013)

[b] Includes the jaguar *Panthera onca*, originally distributed in the Pampa and Atlantic Forest, but now extinct in the former, and the giant-otter *Pteronura brasiliensis*, which is extinct in both domains in Rio Grande do Sul

[c] The recently recognized *Myotis pampa* is probably endemic to the Pampean grasslands in Brazil, Argentina, and Uruguay (Novaes et al. 2021); its conservation status remains to be evaluated

[d] *Brachyteles arachnoides* occurs in the state of Paraná

of passive acoustic monitoring for sampling bats in the *Campos Sulinos* (e.g., Ramos Pereira et al. 2022; da Costa and Ramos Pereira 2022) should help to reduce these shortfalls. Although still incipient, such studies have already revealed the occurrence of previously unknown species in the *Campos Sulinos* and some unexpected patterns concerning bat ecological responses to climatic conditions and open physiognomies of the region's landscapes. A good example comes from the big-crested mastiff bat *Promops centralis*. In Brazil, this bat was only known from the Amazon basin and Mato Grosso do Sul, near Paraguay; a recent nationwide acoustic monitoring effort has shown that it is much more widely distributed than previously thought, and, to date, its southernmost records come from the *Campos Sulinos* in the Parque Nacional dos Aparados da Serra (Hintze et al. 2020). Bat composition in specific sites also started to be unveiled. In the highlands of the Aparados da Serra and Serra Geral National Parks (Ramos Pereira et al. 2022), as well as in the lowlands of Alegrete, Cacequi, and Quaraí (western Pampa; da Costa 2021), most acoustic signals belong to the genus complex *Eumops/Cynomops/Nyctinomops* (Molossidae), followed by *Eptesicus*, *Myotis*, and *Histiotus* (all Vespertilionidae), and *Molossus* (another Molossidae). Species within each of these genera have similar echolocation calls, which often prevents a more precise identification. Despite this, it is estimated that, in the genera mentioned above, there are at least six additional species of bats to be identified and included in the *Campos Sulinos* checklist, which then could easily exceed 40 species (da Costa 2021).

There are 15 species of Didelphidae (marsupials, Didelphimorphia) in the *Campos Sulinos*, most of which occurring in both the Pampa and the highland grasslands. Examples include the white-eared opossum *Didelphis albiventris*, the black-eared opossum *D. aurita*, the lutrine opossum *Lutreolina crassicaudata*, *Metachirus myosuros*, the water opossum *Chironectes minimus*, the gray and black four-eyed opossum *Philander quica*, *Caluromys lanatus*, *Cryptonanus guahybae*, *Gracilinanus microtarsus*, *Monodelphis dimidiata*, *M. iheringi*, *M. scalops*, *Marmosa paraguayana*, and *Marmosops incanus* (Lange and Jablonski 1998; Cherem et al. 2004; Pedó et al. 2010; Marques et al. 2011; Sponchiado 2011; Iob and Stolz 2013; Cáceres et al. 2013; Dias et al. 2015; Queirolo 2016; Pavan and Voss 2016). The small didelphid *Cryptonanus chacoensis* ranges exclusive in the Pampa and is found in the steppe savanna of westernmost RS (Sponchiado 2011; Queirolo 2016).

Lagomorphs are usually abundant in the *Campos Sulinos*, although only one autochthonous species occurs in the Brazilian territory, the tapeti *Sylvilagus gr. brasiliensis*. In the *Campos Sulinos*, this species is restricted to the highland grasslands within the Atlantic Forest biome (Cherem et al. 2004; Valle et al. 2011; Christoff et al. 2013a; Silva et al. 2019). In addition, the exotic European hare *Lepus europaeus* is widely distributed in the *Campos Sulinos*. This species is native to the grasslands of Eurasia and was introduced in South America in 1880, when individuals from Germany were released in Argentina and Chile for hunting. It later dispersed from Uruguay to southern Brazil in the 1950s and was also intentionally introduced, being currently found in both the Pampa and the Atlantic Forest

Table 11.2 Native primates inhabiting forests of the *Campos Sulinos*, with their dietary guild and conservation status at the global, national or regional level (state of Rio Grande do Sul)

Species	Dietary guild	Conservation status
Alouatta caraya	Folivorous-frugivorous	Near Threatened (Global, IUCN[a]) Endangered (Rio Grande do Sul[b])
Alouatta guariba clamitans	Folivorous-frugivorous	Vulnerable (Global, IUCN[c]) Vulnerable (Rio Grande do Sul[b])
Sapajus nigritus cucullatus	Omnivorous	Near Threatened (Global, IUCN[d]) Near Threatened (Rio Grande do Sul[b])
Brachyteles arachnoides	Frugivorous-folivorous	Critically Endangered (Global, IUCN[e]) Endangered (Brazil, ICMBio[f])

[a] Bicca-Marques et al. (2021)
[b] FZB (2014)
[c] Buss et al. (2021)
[d] Di Bitetti et al. (2020)
[e] Talebi et al. (2021)
[f] Talebi et al. (2015)

(Marques et al. 2011; Kasper et al. 2012; Oliveira et al. 2013; Faria et al. 2015; Cherem and Althoff 2015).

Four primate species are native (but not endemic) to the forests of the *Campos Sulinos* (Table 11.2). The brown howler monkey (*Alouatta guariba clamitans*, Atelidae) and the black-horned capuchin (*Sapajus nigritus cucullatus*, Cebidae) have the widest distributions, occurring in forests in Paraná, Santa Catarina, and northern and eastern Rio Grande do Sul (Culot et al. 2019). The southern muriqui (*Brachyteles arachnoides*, Atelidae) is found only in a small stretch of forest immersed in the northernmost portion of the *Campos Sulinos* in Paraná, close to the border with São Paulo (Culot et al. 2019). Finally, the black-and-gold howler monkey (*Alouatta caraya*, Atelidae) is found in the forests of the western portion of the *Campos Sulinos* in Rio Grande do Sul (Bicca-Marques 2013), with its natural occurrence in adjacent forests of Uruguay still requiring confirmation (Jardim et al. 2020).

To date, a total of 48 autochthonous rodent species are known to occur in the *Campos Sulinos,* eight of them endemic (Table 11.3). Sigmodontine cricetids comprise most of this richness (31 species), following the diversity pattern of rodents in the Neotropics (Patton et al. 2015; Paglia et al. 2012). Three species groups can be distinguished when considering the distribution of species throughout the *Campos Sulinos*. The first comprises species typical of the Atlantic Forest, such as the sigmodontines *Akodon montensis*, *A. paranaensis*, *Brucepattersonius iheringi*, *Castoria angustidens*, *Delomys dorsalis*, *Euryoryzomys russatus*, *Sooretamys angouya*, *Thaptomys nigrita*, and the echimyids, *Euryzygomatomys spinosus*, *Kannabateomys amblyonyx*, *Phyllomys dasythrix*, and *P. medius* (Dalmagro and Vieira 2005; Pedó et al. 2010; Marques et al. 2011; Christoff et al. 2013b; Cherem and Althoff 2015; Luza et al. 2016; Queirolo 2016; Quintela et al. 2017). A second group is typical of the Pampa, including species associated mainly with the lowland and mid-altitude physiognomies of coastal and inland *campos* of the Pampa biome (inland steppes in Rio Grande do Sul and coastal pioneer formations in Rio Grande

Table 11.3 Native rodents recorded in the *Campos Sulinos* and their regional (Rio Grande do Sul, RS), national (BR) and global (IUCN) conservation status

Order Rodentia Bowdich, 1821	RS[a]	BR[b]	IUCN[c]
Suborder Myomorpha Brants, 1855			
Family Cricetidae Fischer, 1817			
Subfamily Sigmodontinae Wagner, 1843			
Tribe Akodontini			
Akodon azarae (Fischer, 1829)	NI	NI	LC
Akodon montensis Thomas, 1913	NI	NI	LC
Akodon paranaensis Christoff, Fagundes, Sbalqueiro, Mattevi & Yonenaga-Yassuda, 2000	NI	NI	LC
Akodon reigi González, Langguth & Oliveira, 1998	NI	NI	LC
Bibimys labiosus (Winge, 1887)	NI	NI	LC
Brucepattersonius iheringi (Thomas, 1896)	NI	NI	LC
Castoria angustidens (Winge, 1887)	NI	NI	LC
Deltamys araucaria Quintela, Bertuol, González, Cordeiro-Estrela, Freitas & Gonçalves, 2017*	NE	NE	NE
Deltamys kempi Thomas, 1917	NI	NI	LC
Necromys lasiurus (Lund, 1841)	NI	NI	LC
Oxymycterus nasutus (Waterhouse, 1837)	NI	NI	LC
Oxymycterus quaestor Thomas, 1903	NI	NI	LC
Scapteromys aquaticus Thomas, 1920	NE	NI	LC
Scapteromys meridionalis Quintela, Gonçalves, Althoff, Sbalqueiro, Oliveira & Freitas, 2014	NE	NI	NE
Scapteromys tumidus (Waterhouse, 1837)	NI	NI	LC
Thaptomys nigrita (Lichtenstein, 1829)	NI	NI	LC
Tribe Oryzomyini Vorontsov, 1959			
Euryoryzomys russatus (Wagner, 1848)	NI	NI	LC
Holochilus brasiliensis (Desmarest, 1819)	NI	NI	LC
Lundomys molitor (Winge, 1887)	NI	NI	LC
Nectomys squamipes (Brants, 1827)	NI	NI	LC
Oligoryzomys flavescens (Waterhouse, 1837)	NI	NI	LC
Oligoryzomys nigripes (Olfers, 1818)	NI	NI	LC
Pseudoryzomys simplex (Winge, 1887)	NE	NI	LC
Sooretamys angouya (Fischer, 1814)	NI	NI	LC
Tribe Phyllotini Vorontsov, 1959			
Calomys laucha (Fischer, 1814)	NI	NI	LC
Calomys tener (Winge, 1887)	NE	NI	LC

(continued)

Table 11.3 (continued)

Order Rodentia Bowdich, 1821	RS[a]	BR[b]	IUCN[c]
Tribe Reithrodontini Vorontsov, 1959			
Reithrodon typicus Waterhouse, 1837	NE	NI	LC
Tribe Wiedomyini Reig, 1980			
Juliomys ossitenuis Costa, Pavan, Leite & Fagundes, 2007	NE	NI	NE
Juliomys ximenezi Christoff, Vieira, Oliveira, Gonçalves, Valiati & Tomasi, 2016*	NE	NI	NE
Wilfredomys oenax (Thomas, 1928)	EN	EN	EN
Sigmodontinae *incertae sedis*			
Delomys dorsalis (Hensel, 1872)	NI	NI	LC
Suborder Hystricomorpha Brandt, 1855			
Family Caviidae Fischer, 1817			
Cavia aperea Erxleben, 1777	NI	NI	LC
Cavia magna Ximenez, 1980	VU	NI	LC
Hydrochoerus hydrochaeris (Linnaeus, 1766)	NI	NI	LC
Family Cuniculidae G. S. Miller and Gidley, 1918			
Cuniculus paca (Linnaeus, 1766)	VU	NI	LC
Family Dasyproctidae Bonaparte, 1838			
Dasyprocta azarae Lichtenstein, 1823	VU	NI	DD
Family Erethizontidae Bonaparte, 1845			
Coendou spinosus (Cuvier, 1823)	NI	NI	LC
Family Ctenomyidae Lesson, 1842			
Ctenomys flamarioni Travi, 1981*	EN	EN	EN
Ctenomys lami Freitas, 2001*	EN	EN	VU
Ctenomys minutus Nehring, 1887	NI	VU	DD
Ctenomys ibicuiensis Freitas, Fernandes, Fornel & Roratto, 2012*	NE	NI	DD
Ctenomys torquatus Lichtenstein, 1830	NI	NI	LC
Family Echimyidae Gray, 1825			
Subfamily Dactylomyinae Tate, 1935			
Kannabateomys amblyonyx (Wagner, 1845)	NI	NI	LC
Subfamily Echimyinae Gray, 1825			
Phyllomys dasythrix Hensel, 1872	NI	NI	LC
Phyllomys medius (Thomas, 1909)	NI	NI	LC
Phyllomys sulinus Leite, Christoff & Fagundes, 2008	NI	NI	DD
Subfamily Eumysopinae Rusconi, 1935			
Euryzygomatomys spinosus (Fischer, 1814)	NI	NI	LC
Subfamily Myocastorinae Ameghino, 1902			
Myocastor coypus (Molina, 1782)	NI	NI	LC

Asterisks indicate endemic species

DD Data Deficient, *LC* Least Concern, *EN* Endangered, *VU* Vulnerable, *NE* not evaluated, *NI* not included in any threat category

[a] FZB (2014)

[b] ICMBIO (2018)

[c] IUCN (2021)

do Sul and southernmost Santa Catarina). This group comprises the hystricomorph genus *Ctenomys* (tuco-tucos), with three endemic species (*C. flamarioni*, *C. ibicuensis*, and *C. lami*) (Fernandes et al. 2007; de Freitas et al. 2012; Cordeiro-Estrela and Freitas 2013; Queirolo 2016), plus *Cavia magna* (González and Martínez-Lanfranco 2010; González 2016). In addition, this group also includes sigmodontines that are endemic to the Pampa biome, such as *Akodon reigi*, *Deltamys kempi*, and *Scapteromys tumidus* (D'Elía and Pardiñas 2015; Pardiñas et al. 2015; Pardiñas and Teta 2015). A third group comprises wide-ranging species without clear associations with any specific physiognomy, such as the capybara (*Hydrochoerus hydrochaeris*), paca *Cuniculus paca*, agouti *Dasyprocta azarae*, dwarf porcupine *Coendou spinosus*, and coypu *Myocastor coypus* (Cademartori et al. 2002; Marques et al. 2011; Cordeiro-Estrela and Freitas 2013; Cherem and Althoff 2015; Queirolo 2016).

The heterogeneous vegetation cover of the *Campos Sulinos* (Overbeck et al. 2007) results in marked differences in species abundance patterns of rodent assemblages both between (Pampa vs. highland grasslands of the Atlantic Forest) and within biomes (e.g., Araucaria Forests vs. grasslands; *restinga* forest vs. coastal grasslands). For example, while *Oligoryzomys nigripes*, *Akodon montensis*, and *Delomys dorsalis* are the most abundant species in the highland grasslands, *Deltamys kempi* and *Oligoryzomys flavescens* are numerically more representative in the lowland Pampa biome (Sponchiado et al. 2012; Gonçalves et al. 2014).

Information on ungulates in the *Campos Sulinos* is very scarce, as few inventories on medium and large-sized mammalian fauna are available. Five cervid species have been recorded: *Mazama americana* (red brocket), *Mazama gouazoubira* (brown brocket), *Mazama nana* (pigmy brocket), *Ozotocerus bezoarticus* (pampas deer), and *Blastocerus dichotomus* (marsh deer) (Table 11.4). *Mazama americana* occurs from southern Mexico to northern Argentina. This species is associated mainly with forest habitats but can also use adjacent open areas (Duarte et al. 2012a).

Table 11.4 Native ungulates recorded in the *Campos Sulinos*, with their conservation status in Rio Grande do Sul (RS), Brazil (BR), and globally (IUCN)

Species	RS[a]	BR[b]	IUCN[c]
Family Tapiriidae Gray, 1821			
Tapirus terrestris (Linnaeus, 1758)	CR	VU	VU
Order Artiodactyla Owen, 1848			
Family Cervidae Goldfuss, 1820			
Blastocerus dichotomus (Illiger, 1815)	CR	VU	VU
Mazama americana (Erxleben, 1777)	EN	NI	DD
Mazama gouazoubira (Fischer, 1814)	LC	NI	LC
Mazama nana (Hensel, 1872)	EN	VU	VU
Ozotoceros bezoarticus (Linnaeus, 1758)	CR	VU	NT

DD Data Deficient, *LC* Least Concern, *EN* Endangered, *VU* Vulnerable, *CR* Critically Endangered, *NT* Near Threatened, *NI* not included in any threat category (e.g., LC, DD, or NE)

[a] FZB (2014)

[b] ICMBIO (2018)

[c] IUCN (2021)

In the *Campos Sulinos*, the occurrence of *M. americana* is mentioned for the Araucaria forest/*campos* mosaics in northeastern Rio Grande do Sul (Marques et al. 2011). *Mazama gouazoubira* occurs from southern Amazon to Uruguay and northern Argentina. It shows high plasticity regarding habitat use, occurring in both forests and open areas (Duarte et al. 2012b). In the *Campos Sulinos*, the occurrence of *M. gouazoubira* is associated with the Pampa, *campos*/Araucaria forest mosaics (Marques et al. 2011; Duarte and Cerveira 2013), and grasslands of Santa Catarina (Cherem and Althoff 2015) and Paraná (Duarte et al. 2012b). *Mazama nana* is the smallest cervid in Brazil, reaching an average weight of 15 kg. It is strictly associated with the Araucaria forest and its ecotones with other forest types and Cerrado. The distribution of *M. nana* is restricted to southern Brazil and adjacent areas of Paraguay and Argentina (Duarte et al. 2012c). In the *Campos Sulinos*, *M. nana* is mentioned for the grasslands/Araucaria forest mosaics of northeastern Rio Grande do Sul (Marques et al. 2011; Duarte and Cerveira 2013) and central-eastern Paraná (Duarte et al. 2012c).

The historical distribution of the Pampas deer *Ozotocerus bezoarticus* extended from the southern Brazilian Amazonia to Bolivia and central-eastern Argentina. Currently, the species occurs disjunctly throughouth its historical range, with the largest population living in the Brazilian Pantanal (Duarte et al. 2012d). In the *Campos Sulinos*, relict populations persist in two areas (Duarte et al. 2012d) separated by ca. 600 km. One is the highland grasslands/Araucaria forest mosaics in northeastern Rio Grande do Sul (Duarte and Cerveira 2013) and south-central Santa Catarina (Mazzolli and Benedet 2009). The other is the steppe domain in the Pampa (Duarte and Cerveira 2013).

The marsh deer *Blastocerus dichotomus* originally ranged from southern Amazonia to Cisandine Peru, northeastern Argentina, and eastern Uruguay. Currently, isolated populations persist mainly in the floodplains of some large rivers and their tributaries (Duarte et al. 2012e). In the *Campos Sulinos*, *B. dichotomus* is restricted to a relict population in the Banhado dos Pachecos wildlife refuge (Duarte et al. 2012f), in the Pampa. Forty years ago, the population of *B. dichotomus* in this area was estimated at eight individuals (Voss et al. 1981). There is no current information on the status of this population (Duarte and Cerveira 2013). The axis deer or chital, *Axis axis*, is native to Asia and has been introduced in many areas throughout the world, including South America. Recent data shows that the Uruguayan population is spreading towards the lowlands of the *Campos Sulinos* in southwestern Rio Grande do Sul (Sponchiado et al. 2011).

In addition to cervids, there is an isolated record of *Tapirus terrestris* based on a specimen (MSCJ 56) from Campo Alegre (Cherem et al. 2004), a municipality located in a small and isolated area of the *Campos Sulinos* in northeastern Santa Catarina. The authors did not mention the collection date or any additional information on this specimen. For this reason, the current status of the tapir in the grasslands of northeastern Santa Catarina should be further investigated.

Among the Xenarthra, there are four species of Cingulata in the *Campos Sulinos*, two of them with restricted geographical distribution: the Southern long-nosed armadillo (*Dasypus septemcinctus hybridus*, according to Feijó et al. 2018) and the greater naked-tailed armadillo (*Cabassous tatouay*). None is endemic to the *Campos Sulinos*. The former is found more frequently in the *Campos Sulinos* (Abba et al. 2011), with a distribution restricted to parts of Argentina, Uruguay, Paraguay, and southern Brazil (Abba and Gonzalez 2014). The latter is distributed from northeastern Brazil south to southeastern Paraguay and northeastern Uruguay (Feijó and Anacleto 2021). The other two species, *D. novemcinctus* (nine-banded armadillo) and *Euphractus sexcinctus* (six-banded armadillo), have a wide distribution throughout the Neotropics. In addition to the armadillos, there are two species of anteaters (Pilosa) in the *Campos Sulinos*: *Myrmecophaga tridactyla* (giant anteater) and *Tamandua tetradactyla* (lesser anteater). While the giant anteater is now rare and almost extinct (Tortato and Althoff 2011), the lesser anteater occurs more frequently (but still in low abundance) in the *Campos Sulinos* (Espinosa et al. 2016). Anteaters are found in open-grasslands and savannas, inhabiting all major biomes of South America, and occurring sympatrically throughout most of their geographic ranges (Paglia et al. 2012; Laino et al. 2020).

11.3 Speciation and Hybridization Events

As mentioned above, the *Campos Sulinos* contain hybrid zones where the geographic distributions of closely related species overlap, promoting interbreeding. This process is frequent among carnivorans. A hybrid zone between the southern tiger cat (*Leopardus guttulus*) and Geoffroy's cat (*L. geoffroyi*) is recognized in the ecotone between the Atlantic Forest and the Pampa (Trigo et al. 2008, 2014), with hybrids showing higher tolerance to habitat alteration (e.g., mosaics of cropland areas and remnants of natural vegetation) than parental types (Sartor et al. 2021). A southward expansion of hybrids into the *L. geoffroyi* distribution would compromise the latter's persistence. In addition, a species of wild cat belonging to the Pampas cat complex was recently revalidated (from *Leopardus colocolo* to Muñoa's Pampas cat, *L. munoai*) (Nascimento et al. 2021). This species is endemic to the *Campos Sulinos* and adjacent grasslands, occurring only in the Uruguayan Savanna ecoregion (Nascimento et al. 2021; Tirelli et al. 2021).

Two contact zones between *Alouatta caraya* and *A. guariba clamitans* have been reported in the transition of the *Campos Sulinos* to the westward extension of the Atlantic Forest in central Rio Grande do Sul (Aguiar et al. 2014; Bicca-Marques et al. 2008). The supposed hybridization between these taxa, inferred from individuals with mosaic pelage color (Bicca-Marques et al. 2008; Silva 2010), was confirmed by analyses of mtDNA and Y-chromosome (SRY gene) sequences and diagnostic microsatellite loci (Mourthé et al. 2019). Given that both are forest-dependent taxa, it has been suggested that habitat fragmentation promoted by agribusiness keeps them separated in these contact zones, rather than facilitating the formation of interspecific groups that lead to hybridization (Bicca-Marques et al. 2008).

From an evolutionary perspective, patterns of occurrence in the Pampa lowlands and the Atlantic Forest highlands of the *Campos Sulinos* are quite interesting for rodents, particularly considering the elevation gradient between these biomes, separated by the high elevation, steep, and heterogeneous relief of the Serra Geral. For example, the sigmodontine *Deltamys* and *Scapteromys* include recently diverged (<1 million years) sister species exclusive to either the Pampa or the Atlantic Forest grasslands (Quintela et al. 2014a, 2017; Peçanha et al. 2020). *Deltamys kempi* and *Scapteromys tumidus* are highly abundant in the lowlands and share a common ancestor, respectively, with *D. araucaria* and *S. meridionalis* of higher altitudes (>900 m). In contrast, other sigmodontines, such as *Oxymycterus nasutus*, have populations distributed in both lowland and highland grasslands (Peçanha et al. 2017), with small levels of divergence. These examples of lineages split by the Serra Geral are compatible with the speciation hypothesis in the *Campos Sulinos*. In addition, the tuco-tucos (*Ctenomys*) endemic to *Campos Sulinos* represent a unique model for studying mechanisms underlying speciation. Intra- and interspecific hybrid zones were identified in species of the coastal plain of Rio Grande do Sul and Santa Catarina, which have been monitored for more than 30 years (de Freitas 2021).

11.4 Adaptations to Living in Open Habitats

In the course of their evolution, mammals have developed many adaptations for living in open environments (Feldhamer et al. 2007). These adaptations can be seen in the dentition to feed on herbaceous plants (e.g., Harris and Cerling 2002; Mendoza and Palmquist 2008), in the size of the limbs for locomotion among cursorial species (e.g, Kappelman 1988; Schellhorm and Sanmugaraja 2014), and in physiological and behavioral traits used to communicate and avoid predators (e.g., Randall 1993; Ey and Fischer 2012).

Morphological and other adaptations exhibited by Carnivorans include the light-grey fur with long hairs of varying lengths of the Muñoa's Pampas cat (*Leopardus munoai*), which resembles the dry grasslands or haystacks where it lives. The species' common names in Portuguese ("gato-palheiro") and Spanish ("gato del Pajonal") highlight this trait. The camouflage with the environment conferred by this pelage allows individuals to remain undetected while standing still (F. Tirelli, pers. obs.). It also increases the efficiency of their ambush hunting techniques when preying on rodents (e.g., Brazilian guinea pig *Cavia aperea*) and birds in open grasslands (Migliorin et al. 2018). While the behavior of standing still was advantageous during the evolution of this species, it has proven to be disadvantageous in the human-modified Pampa, where individuals are killed by domestic dogs or victims of roadkills (Tirelli et al. 2021). Other adaptations to live in open habitats include the large ears and light-grey fur of the Pampas fox (*Lycalopex gymnocercus*), making it easier to hear mates or puppies over long distances and hide in the pasture, respectively. The long legs relative to the body length of the maned wolf (*Chrysocyon brachyurus*) allow long-distance movements across grassy and shrubby environments. This adaptation adds to large ears giving it a high vantage point from which to hunt ground-dwelling birds and rodents (Dietz 1985). All those species are mostly diurnal or cathemeral. The Molina's hog-nosed skunk (*Conepatus chinga*), on the other hand, is nocturnal and has long nails allowing the predation of soil insects in open environments (Kasper et al. 2009; Rodrigues 2013).

Among bats, several species of Molossidae are adapted to forage in the open landscapes typical of the *Campos Sulinos*. However, because they fly at high altitudes in the aerosphere (Fenton and Griffin 1997; Kalko et al. 2008), they may occur in areas characterized by dense forests as well. The only species supposed to be endemic to the Uruguayan Savanna, although not yet recorded in the *Campos Sulinos* (*Myotis pampa*), does not appear to be specifically adapted to grasslands, as most species of this genus usually forage on edges between cluttered and open environments. The few individuals identified as belonging to this species in museum collections have been captured with mist-nets near watercourses in localities of the Uruguayan Pampas at altitudes between 30 and 240 m (Novaes et al. 2021). Bats from the *Campos Sulinos* highlands are known to be active at temperatures as low as 8 °C (Ramos Pereira et al. 2022), which probably is a minimum for Brazilian bats, although in landscapes of the Cerrado and Pantanal bats have been recorded active at temperatures as low as 10 °C (M. J. Ramos Pereira, pers. obs.).

In the highlands of the *Campos Sulinos*, where the daily temperature range is very wide, even in summer, and nights are particularly cool, small endotherms like bats face strong challenges to avoid heat loss. Ramos Pereira et al. (2022) have shown that larger bats are able to remain active under temperatures where the activity of smaller bats has already halted, as expected given the relationship between body size and metabolism. Interestingly, however, larger bats forage at higher temperatures compared to smaller bats; this may be explained by the thermal convection process occurring in highland grasslands, which may increase prey availability at higher altitudes, where such larger bats (Molossidae) are known to forage. Does the same pattern occur in other ecosystems and vegetation physiognomies, or is this a particularity of the *Campos Sulinos* highlands? Only further studies will be able to answer this question. In the lowlands, da Costa and Ramos Pereira (2022) showed that different species of insectivore bats perceive the landscape differently, but this is not associated with their foraging guild – open- or edge-space forager –, and that the site occupancy probability by bats in this landscape can be high, suggesting that the mosaic of grasslands of the *Campos Sulinos* lowlands is reasonably favourable to aerial insectivore bats.

No species of primate that inhabits the forests of the *Campos Sulinos* shows adaptations for living in open ecosystems. However, *Sapajus nigritus* is the most prone to broadening its feeding niche by using resources found on the ground, including cultivated plants, food supplemented by people, and food remains found in human garbage. All four species can travel short distances on the ground to visit nearby forest patches, particularly when occupying disjunct home ranges, or longer distances during dispersal. Regarding pelage color, an untested and so far undisputed hypothesis proposes that living in forest islands immersed in a grassland matrix may have played a role in the independent evolution of sexual dichromatism in the two non-sister howler monkey taxa of the *Campos Sulinos* (Bicca-Marques and Calegaro-Marques 1998; Van Belle and Bicca-Marques 2015). Finally, when using grasslands or other open ecosystems, all species are vulnerable to terrestrial predators, such as wild felids, canids, and domestic dogs.

Concerning rodents, the phylotines *Calomys laucha* and *C. tener* occur exclusively in open/dry and grassland biomes, including the Pampa domain within the *Campos Sulinos* (Almeida et al. 2007; Haag et al. 2007; Cordeiro-Estrela and Freitas 2013; Quintela et al. 2014b). They show typical rodent phenotypes. Other rodent species exhibit semiaquatic habits to occupy wetland environments (like *Scapteromys aquaticus*, Bonvicino et al. 2013, and *Holochilus* sp., Torres et al. 2020). On the other hand, *Ctenomys* species show many adaptations to subterranean life, mainly in their claws, forelimbs (scratch-digging), and the skull and incisor teeth (Steiner--Souza et al. 2010; Elissamburu and de Santis 2011; Galiano et al. 2016; Borges et al. 2017; Echeverría et al. 2019). Other species also show adaptations for living below ground, such as tails slightly shorter than body length, small eyes and ears, and tapered snout, or exhibit semi-fossorial habits (e.g., *Bruccepattersonius iheringi* and *Oxymycterus nasutus*; Oliveira and Bonvicino 2006).

11.5 Ecosystems Services and Mammal Conservation

Most carnivoran species are predators; as such, they control populations of their prey and indirectly control populations of species on which their prey feed, contributing to the maintenance of biodiversity and various ecological processes through numerous paths of the food web (McCann et al. 1998). Many species of carnivorans of the *Campos Sulinos* prey on rodents, including exotic species such as house mouse *Mus musculus* and house rat *Rattus*, and control insect populations and potential disease reservoirs (Rodrigues and Chiarello 2018; Bogoni et al. 2020). The Geoffroy's cat (*Leopardus geoffroyi*) and the margay cat (*L. wiedii*) are good examples of species specialized in preying on rodents (Sousa and Bager 2008; Trigo et al. 2013; Migliorini et al. 2018). Exotic rodents successfully colonized almost all environments and are commonly regarded as pests in many agricultural and urban systems, spreading parasites and diseases (Musser et al. 2021; Kryštufek et al. 2021). Some carnivorans are also seed dispersers and contribute to vegetation dynamics, such as the crab-eating fox (*Cerdocyon thous*) (Rocha et al. 2004).

Over 63% of the carnivorans in the *Campos Sulinos* are threatened with extinction, and some are regionally extinct. The Muñoa's Pampas cat (*Leopardus munoai*) is categorized as Endangered (Rio Grande do Sul 2021; Tirelli et al. 2021). This specialized and endemic cat was the only mammal species included in the first Territorial Action Plan for the Pampa, *PAT Campanha Sul e Serra do Sudeste* (Rio Grande do Sul 2021).

Armadillos and other herbivorous burrowing species cause bioturbation, thereby facilitating plant recruitment by changing the physical and chemical properties of the soil when bringing nutrients from deeper layers to the surface (Davidson et al.

2012; Rodrigues and Chiarello 2018). Therefore, they are ecosystem engineers (Desbiez and Kluyber 2013). The Cingulata species have low metabolism, and while living in the ground are vulnerable to burning, habitat conversion into croplands, and terrestrial predators, including domestic dogs (Galetti and Sazima 2006) and possibly the wild boar (Hegel et al. 2019).

In addition to being seed dispersers (Benedicto 2015), primates, particularly howler monkeys in the *Campos Sulinos*, are sentinels of the circulation of the yellow fever virus (Bicca-Marques 2009; Freitas and Bicca-Marques 2011). Infectious diseases are one of the main causes of population decline in primate species (Estrada et al. 2017). Primate conservation in the *Campos Sulinos* requires protecting the remaining forests and reestablishing their historical connections, as larger forests harbor larger and more viable, self-sustaining populations. Small populations living in spatially restricted habitat patches are more prone to extirpation due to the risks associated with travelling or dispersing on the ground (Bicca-Marques et al. 2020). The hazards involved in the recolonization of small habitat patches embedded in natural grasslands or open anthropogenic ecosystems following population extirpation caused by disease outbreaks, such as yellow fever, pose a significant threat to primate conservation in fragmented landscapes (Bicca-Marques 2009; Freitas and Bicca-Marques 2011).

Most bat species of the *Campos Sulinos* are insectivores and, therefore, important agents of control of agricultural pests (Cleveland et al. 2006; Reiskind and Wund 2009). This service is estimated to account for annual savings of US$ 390.6 million per harvest of corn, particularly in the Brazilian Cerrado (Aguiar et al. 2020). Although no similar estimate exists for crops established in the *Campos Sulinos*, there is no reason to believe that insectivorous bats do not provide a service equally valuable in this unique landscape.

The recently described *Myotis pampa*, whose type locality is Artigas (Uruguay), on the border with Quaraí (Brazil) and Entre Ríos (Argentina), is probably endemic to the Uruguayan Savana, likely occurring in the grasslands of these three countries (Novaes et al. 2021). The region is known to host several endemic plants and animals (Pillar et al. 2016) but remains one of the least studied ecoregions with regard to bat fauna (Bernard et al. 2011). Although the conservation status of *M. pampa* has not yet been evaluated, this species is probably under some level of threat due to its restricted distribution in a region under increasing anthropogenic pressure. Also, several bat species have not been evaluated for their regional conservation status, and others are categorized as “Data Deficient”. Non-existent, incomplete, or unsatisfactory data, and the lack of basic biological and ecological information, including occurrence patterns, habitat preferences and population sizes, are per se a threat to the persistence of populations of these species in the region.

Finally, changing the narrative on bats and diseases for people and domesticated animals is also fundamental. Controlling deaths and exposures to rabies through vaccination of reservoir animals, such as cattle, domestic dogs, and even terrestrial wildlife, has been highly successful in Mexico, the United States, and Uruguay (Anderson et al. 2014; Botto Nuñez et al. 2019; Pieracci et al. 2019), and should be mirrored in regions where livestock production is a major economic activity, such as the whole South American grasslands. Apart from their well-known association with rabies, bats have received enormous attention in the last couple of years in the context of coronaviruses because they carry a great variety of such viruses, of which they are natural and ancestral reservoirs (Ge et al. 2016). Reports of cases of persecution and destruction of bat roosts, as well as the culling of bat populations have increased around the world (Fenton et al. 2020; Zhao 2020), negatively affecting populations of this group and the irreplaceable ecosystem services that they provide (Kunz et al. 2011).

We now know that zoonotic spillovers are mostly the consequence of severe anthropogenic landscape changes, often resulting from intensive livestock and agricultural production. Indeed, the reduction in the number of native species and their habitats seems to be a much more direct cause of the spread of diseases of wildlife origin (Ezenwa et al. 2006; Keesing et al. 2010; Doughty et al. 2020). In a region where traditional agricultural activities are themselves at risk of disappearing, perhaps it is time for South American conservationists and landowners to follow the One Health approach, recognizing the interconnectedness of people, animals, and the environment, and engaging stakeholders and experts from multiple disciplines to work together locally, regionally, and nationally to achieve the best health for all three.

Similarly, some didelphids are vulnerable to extinction at the regional scale, particularly due to habitat fragmentation associated with intensive agricultural and silvicultural activities. This is the case of the lutrine opossum and the water opossum, *Metachirus myosurus* and *Marmosa paraguayana* (FZB 2014; IMA 2011).

Despite their abundance, some rodents of the *Campos Sulinos* suffer several anthropogenic impacts due to their small geographic ranges and strict habitat associations. The endemic subterranean tuco-tuco *C. flamarioni* and the wiedomyine *Wilfredomys oenax* are considered endangered in the *Campos Sulinos*. The intensive agricultural and silvicultural activities, as well as urbanization, sand mining, and the introduction of domestic animals, have been suspected to impact populations of these species (Fernandes et al. 2007; de Freitas et al. 2012; Bonvicino et al. 2018; Christoff 2018). Additionally, other species are considered locally threatened in some parts of their range mainly because of hunting pressure and habitat loss, as is the case of the agouti (*Dasyprocta azarae*), paca (*Cuniculus paca*), Brazilian guinea pig (*Cavia magna*), and the tuco-tuco *Ctenomys lami* (FZB 2014).

One exotic Artiodactyla is increasing its occupation of the *Campos Sulinos*. The invasive alien axis deer or chital *Axis axis* is native to Asia (India, Nepal, Bhutan, Bangladesh, and Sri Lanka) and has been introduced in several places in Europe, Australia, and North and South America (Randel and Tomečev 2021). In the *Campos Sulinos*, free-ranging individuals of *A. axis* have been recorded in the Espinilho State Park (Sponchiado et al. 2011), in the vicinity of Taim Ecological Station (Quintela, pers. obs.), and in the Serra do Caverá, Alegrete and Cerro do Jarau, Quaraí (F. Tirelli and M.J. Ramos Pereira pers. obs.), in areas of steppic savannah and pioneer formations of the Pampa biome. Another invasive artiodactyl is the wild boar (*Sus scrofa*), widely distributed in the *Campos Sulinos* (Pedrosa et al. 2015). Considering the potential impacts of these two species (Quintela et al. 2010; Etges 2016), urgent monitoring and control measures are recommended.

Actions for conserving biodiversity in the *Campos Sulinos* formulated up to the 2000s were based almost exclusively on the pattern of greater diversity in intermediate to high levels of grazing or burning found for plants (Pillar and Vélez 2010; Overbeck et al. 2007). That said, it is no surprise that the topic 'conservation' did not emerge in the modeling presented in the introduction, as knowledge about mammal response to disturbances was incipient at that time. Recent research in the *Campos Sulinos* has provided new insights into the conservation of biodiversity in the region (e.g., Luza et al. 2014; Carlucci et al. 2016). Several small-bodied mammals – and other vertebrates and woody plants – are more likely to occur in tall grasslands and shrublands than in short grasslands (Pedó et al. 2010; Luza et al. 2016, 2018). These new insights value mosaics of tall and short vegetation across the landscape to maximize the chance of conserving a wider range of taxa (Hobbs and Huenneke 1992; Erdós et al. 2020). To achieve the conservation of mosaics, the proposal involves the creation of strictly protected areas to conserve ecological processes, and sustainable use areas to conserve ecological patterns at light levels of disturbance (Dudley 2008). In this system, private areas could also contribute to the conservation of ecological patterns even at high levels of disturbance.

The systematic conservation planning of Lima et al. (2020) is a first effort to reconcile these two perspectives in the geographical space to prioritize grassland conservation areas in the Pampa biome. While considering environmental and socioeconomic factors, these authors basically simulated the positioning of different proportions of strictly protected and sustainable use areas to achieve conservation of 17% of the Pampa (as recommended in the 11th Aichi target). They found four nuclei of irreplaceable importance for conserving grassland cover. The formulation of a parallel between our mapping of scientific knowledge (Fig. 11.1c) and the nuclei identified by Lima et al. (2020) allows us to check if scientific knowledge exists in regions with high ecological and conservation importance. The nuclei of northwestern and central Pampa have none to incipient scientific knowledge about mammals, whereas the nuclei of the western and southernmost Pampa have more availability of scientific knowledge. Thus, only a part of the *Campos Sulinos* provides information on mammals to inform future systematic conservation planning. Studies in the northern portion of the *Campos Sulinos*, specifically in the highland grasslands, are urgently needed.

11.6 Research Priorities

Research priorities include several topics and regions. Topics such as conservation, functional diversity, and ecosystem services did not emerge from the literature of mammals produced so far in the *Campos Sulinos*. While we know several aspects of population genetics (e.g., Gonçalves and Freitas 2009), habitat selection (e.g., Sponchiado et al. 2012), the effect of disturbances on species occurrence (Pedó et al. 2010; Luza et al. 2015, 2018, among others), and landscape influence on species site occupancy probability (da Costa and Ramos Pereira 2022), this knowledge is available mostly for small mammals. We have incipient knowledge of population sizes and densities for most mammals in the *Campos Sulinos*, with most information coming from carnivores (e.g., Kasper et al. 2012; Tirelli et al. 2019). An important gap concerns the Xenarthra. The only studies in the region that focuses on Cingulata species is Oliveira et al. (2015) and de Oliveira et al. (2023), mainly focusing on activity patterns and occupancy of *Dasypus novemcinctus*. This taxon is often listed in opportunistic surveys and little is known of its ecology. The same applies to anteaters, for which there are few studies on behavior (Braga et al. 2010) and distribution (Tortato and Althoff 2011; Espinosa et al. 2016).

Functional diversity is an emergent field of research, as it allows us to link occurrence with ecological functions (Luza et al. 2021) and ecosystem services (Bogoni et al. 2020). Research in this field is welcome, as it will certainly increase the perceived value of the contribution of mammals to ecosystem functioning and human well-being.

This chapter provides an overview of the current state of knowledge on mammals in the *Campos Sulinos*. It highlights that this region is not merely a peripheral area in terms of mammal diversity compared to forested biomes located further north. Consequently, the conservation of the *Campos Sulinos* mammals requires targeted initiatives to preserve their populations and maintain the associated ecosystem services, especially in the face of the region's alarming rates of land use change.

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Chapter 12
Fish Diversity and Conservation in a Neotropical Grassland Region

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12.1 Introduction

The grassland region treated herein includes the areas called Pampa in Brazil and *Pastizales del Río de La Plata* in Uruguay and Argentina and the grassland enclaves in the southern part of the Atlantic Forest (Fig. 12.1). It corresponds to one of the largest natural grassland ecosystems in the Neotropics (Azpiroz et al. 2012). This continuous grassland region embraces the southern portion of the state of Rio Grande do Sul, Brazil, the Province of Buenos Aires and the eastern limits of Entre Ríos and Corrientes provinces, in Argentina, and the whole Uruguay. It includes the lower portions and lowland tributaries of four different river drainages: the Uruguay river drainage in the three countries; the tributaries of the Río de La Plata estuary in Uruguay and Argentina; the Patos lagoon drainage in Brazil and Uruguay; and the Tramandaí river drainage in Brazil. It also includes small partions of the headwaters of a few eastern tributaries of

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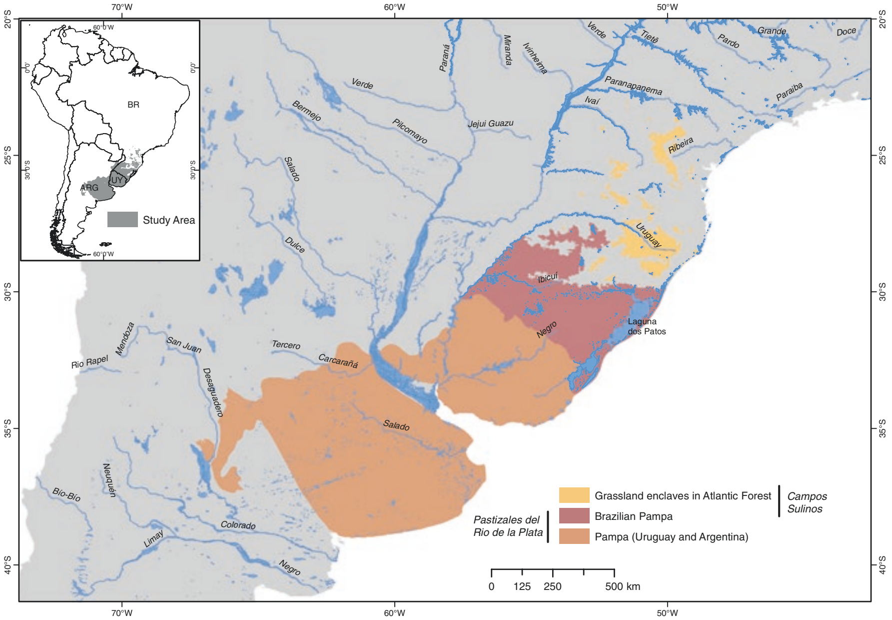

Fig. 12.1 Natural grassland areas in Brazil, Uruguay and Argentina. The region known as *Pastizales del Río de la Plata* includes grasslands in Uruguay, Argentina, and the Brazilian Pampa. The Brazilian Pampa and the highland grassland enclaves located in the Atlantic Forest domain form the region named *Campos Sulinos* (Southern Grasslands) in Brazil

the Paraná river. Such area includes six freshwater ecoregions: Lower Uruguay, Lower Parana, Laguna dos Patos, and Tramandaí-Mampituba, Upper Parana and Iguaçu (Abell et al. 2008; Albert et al. 2011), which are defined primarily by hydrographic (river basin) boundaries, with some boundaries defined by other landscape or physiographic discontinuities. Such is the case of the Lower and Upper Uruguay ecoregions, delimited by the Yucuman waterfalls, as well as the Lower Parana and Iguaçu ecoregions, delimited by the Iguaçu falls (Fig. 12.2).

In our analysis, the Pampa is limited to freshwater drainages north of the Río de La Plata, a region with a high density of freshwater fish samples and inventories (Bertaco et al. 2016; Bessonart et al. 2021). A list of 141 species occurring in the Río de La Plata and its southern tributaries in Argentina is provided by Maiztegui et al. (2022).

Additionally, we briefly compare the freshwater fish fauna of the lowland Pampa with that associated with smaller areas of natural grasslands in the upland plateaus of the Serra Geral geological formation in the states of Rio Grande do Sul, Santa Catarina and Paraná (Brazil) (Fig. 12.1). These highland grasslands are enclaves of open ecosystems located in a region dominated by the Atlantic Forest and, together with the Brazilian Pampa, are called *Campos Sulinos* in Brazil. Unlike the lowland Pampa, which includes large wetlands, small streams and large rivers, the highland grasslands mostly contain fast-flowing headwater streams and small wetlands. They span across five freshwater ecoregions (Abell et al. 2008): Laguna dos Patos, Upper Uruguay, Tramandaí-Mampituba, Iguaçu and Upper Parana (Fig. 12.2).

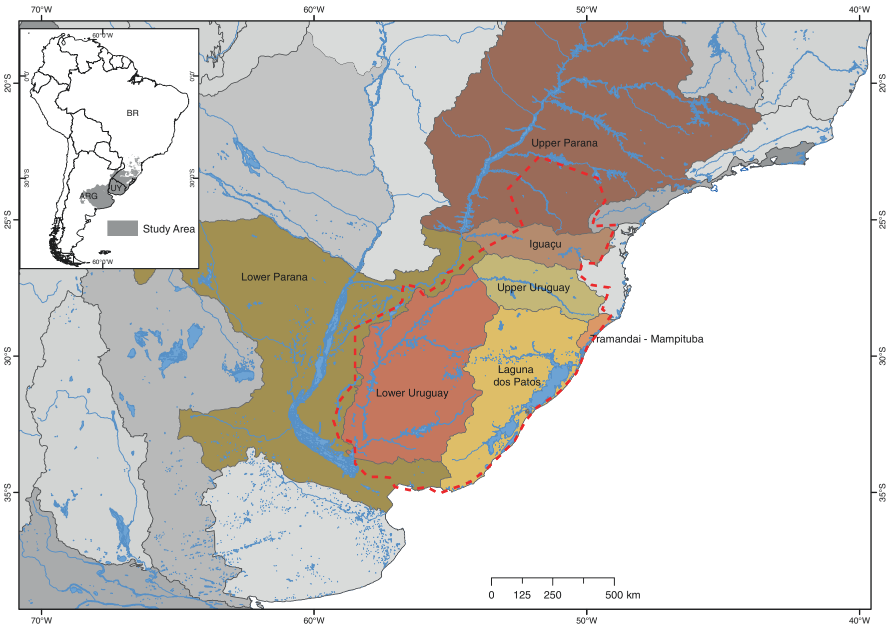

Fig. 12.2 Freshwater ecoregions encompassing grassland areas in Brazil, Uruguay, and Argentina (in brownish colors): Lower Uruguay, Upper Uruguay, Laguna dos Patos, Tramandaí-Mampituba, Upper Parana, Lower Parana and Iguaçu. The red line delimits the approximate area for fish data compiled in this study (only freshwater habitats in grassland regions of southern Brazil, i.e., the *Campos Sulinos*, and the Uruguayan portion of the *Pastizales del Río de la Plata*)

12.2 Freshwater Basins and Freshwater Ecoregions as Constraints for the Freshwater Fish Fauna in the Pampa

There are 334 fish species in the pampean region north of the Río de La Plata. These species are not evenly distributed across the Pampa, so fish assemblages can differ markedly depending on their location in adjacent freshwater ecoregions or within hydrographic basins. Only 15.4% of the species are shared by the Patos lagoon, Uruguay river and Tramandaí river drainages, and few are shared by any two of these drainages (3.9% and 8.4%) (Fig. 12.3). Of the species recorded in the pampean portions of these three drainages, 173 are found only in the Uruguay river, 59 only in Patos lagoon and 8 only in the Tramandaí river watersheds. On the other hand, all species from northern tributaries of the Río de La Plata (included in Lower Parana ecoregion) are shared with the Uruguay river watershed (Bessonart et al. 2021).

Composition dissimilarities are also found within drainage basins, when grassland areas in the lower and upper portions of the same drainage are compared (Fig. 12.4). Only around 31% of the species found in the Uruguay river drainage are shared between the Lower and Upper Uruguay ecoregions, resulting in significant differences in the fish communities inhabiting the lowland Pampa habitats

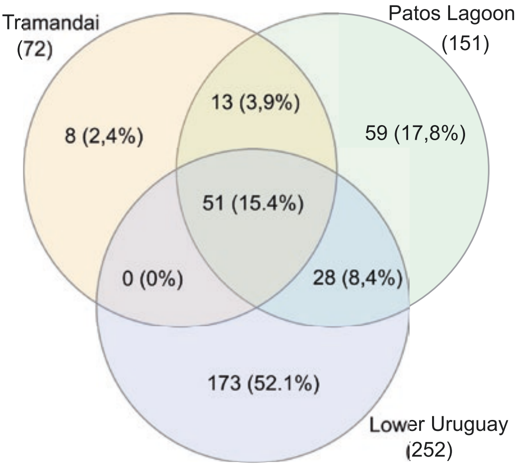

Fig. 12.3 Number of fish species shared between the freshwater ecoregions Laguna dos Patos (LP), Lower Uruguay (LU) and Tramandaí-Mampituba (TM)

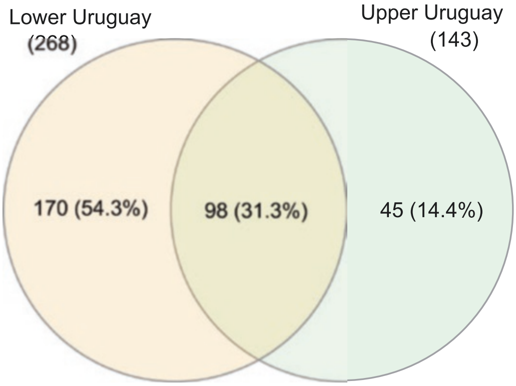

Fig. 12.4 Number of fish species in the Uruguay river drainage, according to their distribution in the Lower and Upper Uruguay freshwater ecoregions

compared to those of the grassland areas located in the highland plateaus of this drainage. For example, considering the most species rich families, there are 49 characid species, 38 loricariid species, and 26 cichlid species found in the lower Uruguay river that do not occur in the upper Uruguay river, and respectively 14, 16, and seven species of these families occurring in the upper Uruguay river that do not occur in the lower Uruguay river. This same pattern of compositional differences between fish faunas of lowlands and uplands within the same basin seems to occur in the Patos Lagoon and in the Tramandaí-Mampituba drainages (Malabarba and Isaia 1992; Becker et al. 2013) (although, unlike the Uruguay river basin, they each constitute a single freshwater ecoregion).

12.3 Endemism

We found that 102 fish species are endemic to the Pampa (30.5% of the total). The freshwater fish fauna endemic to the grasslands of southern Brazil and Uruguay is notable and well-documented (see Bessonart et al. 2021 and Andrade et al. 2023 for the Brazilian and Uruguayan Pampa, and Malabarba et al. 2009 for the highland areas of southern Brazil). The recent study of Andrade et al. (2023) found that fish (i.e., Actinopterygii and Chondrichthyes) have the highest proportion of species restricted to the *Río de la Plata* grassland region (36.7%) among all groups of vertebrates occurring in the area. These species are mainly annual fishes of the genera *Austrolebias* and *Cynopoecilus* (Cyprinodontiformes: Rivulidae), approximately 40 species, which are deeply associated with temporary wetlands of subtropical/temperate grasslands. Even though Cyprinodontiformes represent only 15% of the fish species in the Pampa, they contribute with more than 44% of the endemic species of the region (Figs. 12.5 and 12.6).

Among rivulids, Ferrer et al. (2014) discussed the successful invasion of the Pampa by the subtribe Cynopoecilina. The most basal species of the genus *Cynopoecilus*, *C. notabilis*, inhabits relictual flooded forests in the Pampa, similar to species of the other Cynopoecilina genera *Campellolebias*, *Leptolebias*, and *Notholebias*, which are typically found in the Atlantic Forest biome. The remaining species of *Cynopoecilus*, however, form a clade that successfully diversified into

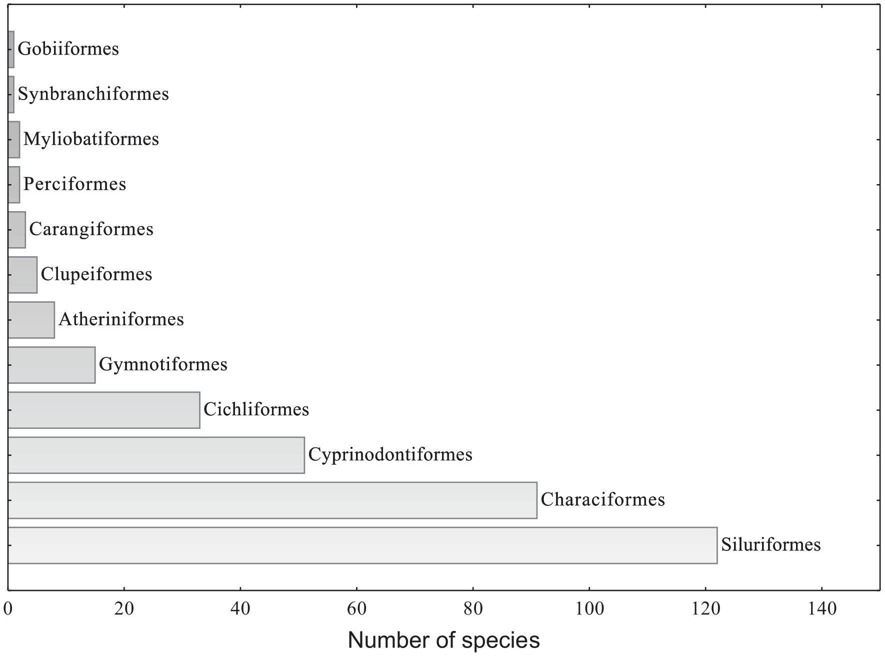

Fig. 12.5 Number of freshwater fish species in the Brazilian Pampa, by order

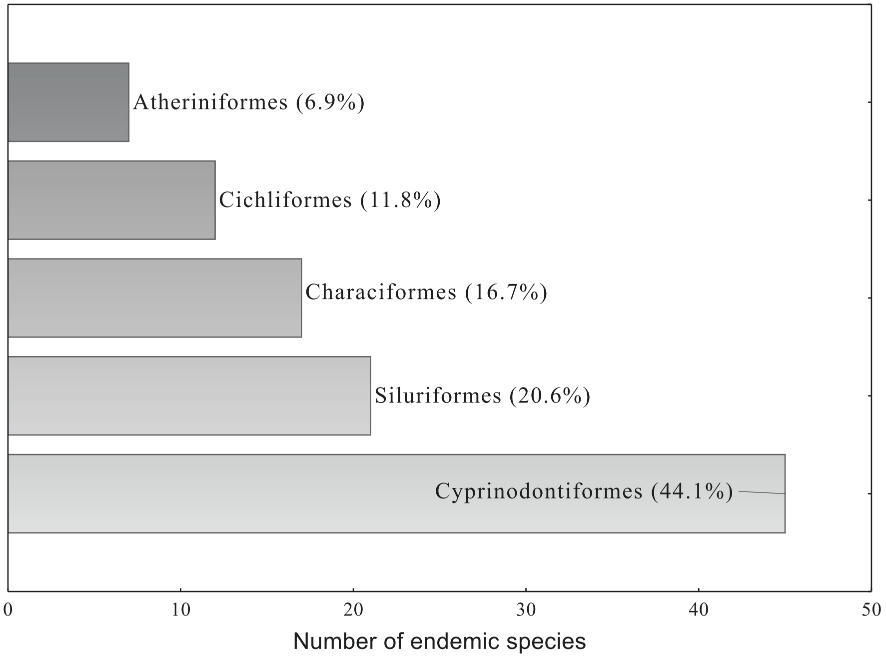

Fig. 12.6 Number of pampean endemic fish species in different orders and their proportion relative to the total number of fish species endemic to the Pampa (102)

several species occupying wetlands within large grassland areas of the Pampa biome. The diversification of annual fishes in grassland ecosystems is even more intense in the genus *Austrolebias*. There are 25 species endemic to the lowland wetlands of the Brazilian and Uruguayan Pampa, which in part also inhabit the *Serra do Sudeste* (154 m a.s.l. in the case of *A. paucisquama*; Ferrer et al. 2008) and even the highland grasslands of southern Brazil (approximately 1000 m a.s.l. in the case of *A. botocudo* and *A. nubium*; Lanés et al. 2021). There are four other species of Cyprinodontiformes restricted to the Pampa: *Cnesterodon decemmaculatus*, *C. holopteros*, and *Phalloceros heptaktinos* (Poeciilidae), and *Jenynsia onca* (Anablepidae). All these "*barrigudinhos*" are small viviparous fish that usually inhabit the densely vegetated margins of shallow streams and swamps (Lucinda et al. 2006a, b; Lanés et al. 2008) (Fig. 12.7).

The catfish genera *Hisonotus* and *Scleronema* (Siluriformes) also underwent an impressive diversification in the *Río de la Plata* grasslands. *Hisonotus* (Loricariidae) includes eight species found in the Pampa, seven of which are endemic: *H. armatus*, *H. charrua*, *H. laevior*, *H. nigricauda*, *H. notopagos*, *H. ringueleti*, and *H. taimensis* (Carvalho and Reis 2009; 2011). These species, along with the two species of *Otocinclus* endemic to the Pampa (*O. arnoldi* and *O. flexilis*), are small-sized hypoptopomatines that live in small streams and associate with submerged vegetation. *Scleronema* (Trichomycteridae) comprises ten small-sized catfish species

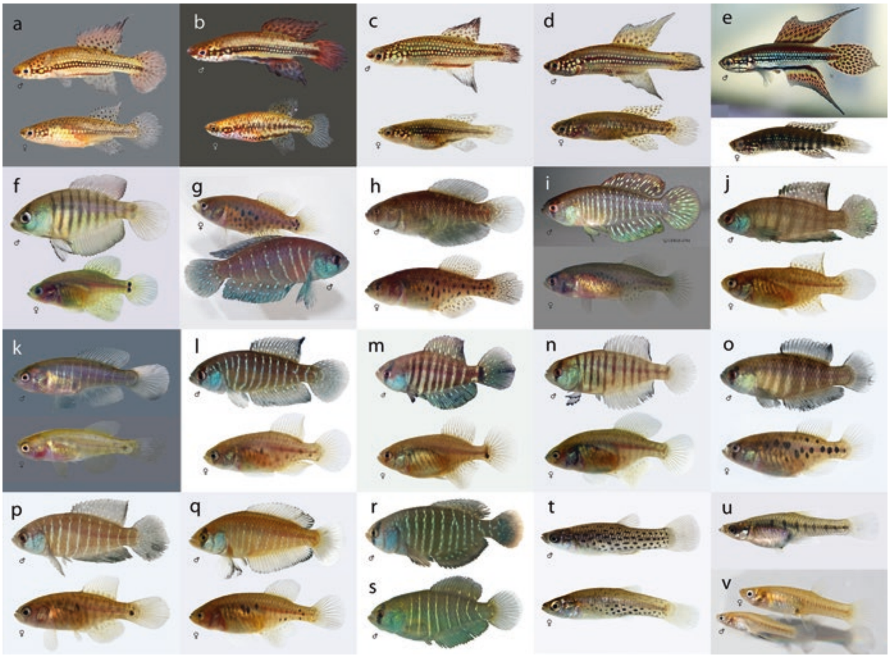

Fig. 12.7 Cyprinodontiformes contain 45 species endemic to the Pampa, corresponding to 41.3% of the fish species endemic to this region. Some of these cyprinodontiforms include the rivulids *Cynopoecilus fulgens* (**a**), *C. intimus* (**b**), *C. melanotaenia* (**c**), *C. nigrovittatus* (**d**), *C. notabilis* (**e**), *Austrolebias adloffi* (**f**), *A. affinis* (**g**), *A. cinereus* (**h**), *A. cyaneus* (**i**), *A. ibicuiensis* (**j**), *A. juanlangi* (**k**), *A. litzi* (**l**), *A. minuano* (**m**), *A. nachtigalli* (**n**), *A. paucisquama* (**o**), *A. periodicus* (**p**), *A. univentripinnis* (**q**), *A. queguay* (**r**), *A. viarius* (**s**); the anablepid *Jenynsia onca* (**t**); and the poeciliids *Cnesterodon decemmaculatus* (**u**) and *Phalloceros heptaktinos* (**v**)

(reaching up to 15 cm in total length) that inhabit the sandy bottom of rivers and streams. Eight of them are found in the Pampa biome, with six showing different degrees of endemism: *S. guapa* and *S. operculatum* are restricted to the Ibicuí River basin; *S. teiniagua* to the Quaraí River basin; *S. ibirapuita* to the Ibirapuitã and Arapey Grande rivers basins; and *S. macanuda* and *S. minutum* to the Uruguay River basin and Patos-Mirim system (Ferrer and Malabarba 2020; Ferrer 2021). Two other trichomycterids, which occupy a habitat similar to that of *Scleronema* species, are endemic to the Pampa: *Ituglanis australis* and *I. inusitatus* (Datovo and de Pinna 2014; Ferrer and Donin 2017) (Fig. 12.8).

The Siluriformes include other seven species endemic to the Pampa biome: two species of *Rineloricaria* (*R. isaaci* and *R. longicauda*; Loricariidae); two species of *Heptapterus* (*H. exilis* and *H. sympterygium*; Heptapteridae); *Listrura depinnai* (Trichomycteridae); *Lepthoplosternum tordilho*, and *Scleromystax reisi* (Callichthyidae) (Reis 1983, 1997; Buckup 1988; Rodriguez and Miquelarena 2008; Villa-Verde et al. 2013; Britto and Reis 2005; Faustino-Fuster et al. 2019). It is interesting to note that *Listrura depinnai* and *Scleromystax reisi* represent the

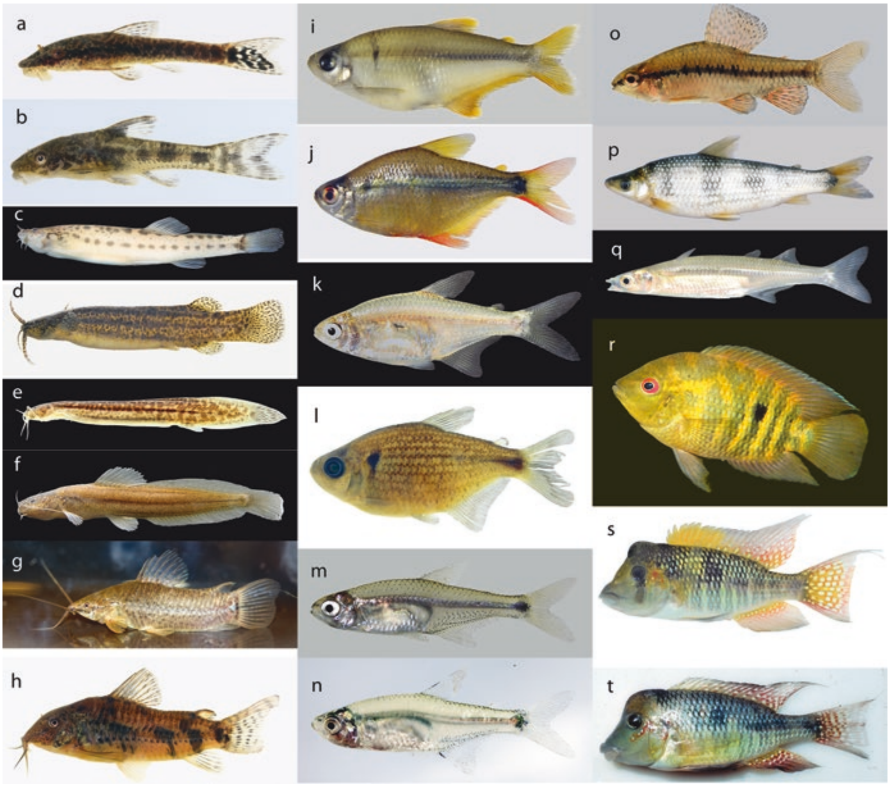

Fig. 12.8 Siluriformes endemic to the Pampa include loricariid species of the genera *Hisonotus* (e.g. *H. armatus*, **a**) and *Otocinclus* (e.g. *O. flexilis*, **b**); trichomycterid species of the genera *Scleronema* (e.g. *S. operculatum*, **c**), *Ituglanis* (e.g. *I. australis*, **d**) and *Listrura depinnai* (**e**); heptapterid species of the genus *Heptapterus* (e.g. *H. sympterygium*, **f**); and the callichthyids *Lepthoplosternum tordilho* (**g**) and *Scleromystax reisi* (**h**). Endemic Characiformes include characid species of the genera *Diapoma* (e.g. *D. terofali*, **i**), *Hyphessobrycon* (e.g. *H. meridionalis*, **j**), *Cheirodon ibicuhiensis* (**k**), *Ectrepopterus uruguayense* (**l**), *Heterocheirodon yatai* (**m**) and *Macropsobrycon uruguayanae* (**n**), crenuchid species of the genus *Characidium* (e.g. *C. rachovii*, **o**), and anostomid species of the genus *Schizodon* (e.g. *S. jacuiensis*, **p**). Endemic Atheriniformes include species of the genus *Odontesthes* (e.g. *O. mirinensis*, **q**). Endemic Cichliformes include species of the genera *Australoheros* (e.g. *A. acaroides*, **r**) and *Gymnogeophagus* (e.g. *G. peliochelynion*, s and *G. pseudolabiatus*, **t**)

southernmost limit to their genera, which include species typically associated with the small coastal river basins of the Atlantic Forest. Consequently, their records are restricted to dense fragments of forest in the Pampa biome (Villa-Verde et al. 2013; Britto and Reis 2005) (Fig. 12.8).

In Characiformes, the genus *Diapoma* (Characidae: Stevardiinae) has five species endemic to the Pampa: *D. alegretense*, *D. pampeana*, *D. speculiferum*, *D. terofali*, and *D. uruguayense* (Malabarba and Weitzman 2003; Ito et al. 2022). All these "*lambaris*" are small-sized species usually found in the lentic stretches of rivers and streams with clear waters. Other characid species strongly associated with the Pampa biome and its habitats are *Cheirodon ibicuhiensis* (rivers, streams, lakes and swamps), *Ectrepopterus uruguayensis* (streams), *Heterocheirodon yatai* (rivers, streams, and lakes), *Hyphessobrycon meridionalis* (swamps and floodplains), *H. togoi* (rivers, streams, lakes, including estuarine zones), *Macropsobrycon uruguayanae* (lakes and floodplains), and *Mimagoniates inequalis* (streams and swamps surrounded by forests) (Jerep and Malabarba 2011; Serra et al. 2014; Lanés et al. 2023) (Fig. 12.8).

The genus *Characidium* (Crenuchidae) includes three small-sized species endemic to the Pampa, which inhabit the lotic areas of rivers and streams (*C. occidentale* and *C. tenue*) or lakes and swamps, associated with aquatic vegetation (*C. rachovii*) (Buckup and Reis 1997). Additionally, the two medium-sized species so-called "*voga*", *Schizodon australis* and *S. jacuiensis* (Anostomidae), live exclusively in the pampean stretches of large rivers within the biome, such as the Uruguai and Jacuí (Fig. 12.8).

The Pampa also harbors seven endemic species of *Odontesthes* (Atheriniformes) originated from a recent radiation related to a marine-to-freshwater transition in the region (Hughes et al. 2020). Interestingly, these species have distinct distributions and degrees of endemism, being adapted to different habitats in the Pampa. For example, *O. bicudo*, *O. ledae*, and *O. piquava* are found exclusively in a few small lakes of the Tramandaí system (Malabarba and Dyer 2002), whereas *O. mirinensis* inhabits the large Patos and Mirim lagoons. In contrast, *O. perugiae* occurs only in the rivers of the La Plata basin (Wingert et al. 2017). The remaining two species, *O. humensis* and *O. retropinnis*, occupy lakes and rivers in the Uruguay and Patos basins (Fig. 12.8).

There are 12 species of Cichliformes endemic to the Pampa, eight being mouth- or substrate-brooding "*carás*" of the genus *Gymnogeophagus* (Reis and Malabarba 1988; Malabarba et al. 2015; Loureiro et al. 2016; Turcati et al. 2018). It is interesting that a pattern similar to that mentioned for *Scleronema* (i.e., species with ranges restricted to one or two eastern sub-basins of the Uruguay River) is observed in *Gymnogeophagus*: *G. missioneiro* from Piratini River basin, *G. peliochelynion* from Arapey Grande River basin, *G. pseudolabiatus* from Quaraí River basin, *G. tiraparae* and G. *meridionalis* from Ibicuí and Negro rivers basins. In contrast, *G. mekinos* and *G. terrapurpura* range in the eastern tributaries of the Uruguay River and the coastal drainages of the Río de La Plata estuary and Atlantic Ocean, like *S. minutum* and *S. macanuda*. Four species of the cichlid *Australoheros* are endemic to the Pampa, with *A. charrua* restricted to the eastern tributaries of the lower Uruguay River basin, *A. facetus* occurring in the coastal drainages of the Río de La Plata estuary, and *A. minuano* and *A. scitulus* inhabiting the Uruguay River basin and some rivers draining to Patos and Mirim lagoons (Říčan and Kullander 2008; Lucena et al. 2022) (Fig. 12.8).

The *campos de altitude* (upland or highland grasslands) of southern Brazil, located in the Serra Geral Formation, belong to a region also called *Planalto das*

Araucárias in Brazil. The rivers and streams of the southern part (Rio Grande do Sul and Santa Catarina states) drain to the upper tributaries of the Uruguay River, Laguna dos Patos and Tramandaí-Mampituba river drainages. The grasslands of the northern region (states of Paraná and São Paulo) include relatively small sections of tributaries of the upper Parana river and Iguaçu river, where only the latter encompasses endemic species: *Ancistrus agostinhoi* (Loricariidae), *Cambeva crassicaudata*, *C. mboycy*, and *C. taroba* (Trichomycteridae) (Wosiacki and Garavello 2004; Wosiacki and de Pinna 2008; Bifi et al. 2009). In contrast, the southern *campos de altitude* harbor 30 endemic species. Most of them are endemic to a single drainage, but a considerable number of species occur along the headwaters of more than one drainage. For example, the characids *Astyanax brachypterygium*, *A. pirabitira*, *Bryconamericus patriciae*, and the anablepid *Jenynsia eirmostigma* inhabit the headwater streams of the Uruguay and Patos drainages; *Cambeva balios* (Trichomycteridae) occurs in the headwaters of these two basins plus the Mampituba River basin; and *A. cremnobates* is found exclusively in the headwaters of the Patos and Maquiné River basins (Ghedotti and Weitzman 1995; Bertaco and Malabarba 2001; da Silva 2004; Lucena et al. 2013; Ferrer 2021).

The number of endemic species of Siluriformes with a preference for fast-flowing stretches of rivers and streams with rocky bottoms in the southern section of the *campos de altitude* is remarkable. The genera *Cambeva* (Trichomycteridae) and *Eurycheilichthys* (Loricariidae) include most of these species (*C. balios*, *C. diatropoporos*, *C. flavopicta*, *C. tropeiro*, *E. coryphaenus*, *E. paucidens*, *E. planus*, and *E. vacariensis*), with *Pareiorhaphis* and *Rineloricaria* having two endemic species each: *P. eurycephalus*, *P. vestigipinnis*, *R. anitae*, and *R. tropeira* (Pereira and Reis 2002; Ghazzi 2008; Ferrer and Malabarba 2013; Reis 2017). The remaining two species of Siluriformes endemic to the southern upland grasslands are the hypoptopomatine *Hisonotus prata* and the heptapterid *Heptapterus carnatus* (Carvalho and Reis 2011; Faustino-Fuster et al. 2019).

In addition, some Characiformes and Cichliformes associated with moderate to fast-flowing streams and rivers are endemic to the southern *campos de altitude*, such as the characids *Astyanax brachypterygium*, *A. cremnobates*, *A. pirabitira*, *A. taurorum*, and *Bryconamericus patriciae*; and the cichlids *Crenicichla igara*, *C. jurubi*, and *C. lucenai* (Lucena and Kullander 1992; Bertaco and Malabarba 2001; da Silva 2004; Mattos et al. 2014; Lucena et al. 2017). Other species endemic to the southern *campos de altitude* are some Cyprinodontiformes of the genus *Cnesterodon* (e.g., *C. brevirostratus* and a number of undescribed species), which inhabit first order streams; and three Rivulidae annual fishes: *Austrolebias botocudo*, *A. nubium*, and *A. varzeae* (Costa et al. 2004; Lanés et al. 2021). Remarkably, *Odontesthes crossognathos* (Atherinopsidae), an endemic silverside occurring in altitudes varying from 750–1000 m a.s.l. in the southern upland grasslands, is one of the species that originated from a recent radiation resulting from a marine-to-freshwater transition of the genus *Odontesthes* (Wingert et al. 2022).

12.4 Fish Diversity Compared to Other Freshwater Ecoregions in South America

Comparison of fish species richness between the Pampa and other major terrestrial biomes in Brazil can be established only tentatively, since aquatic biogeographical units are more adequately defined by the watersheds of large river basins, which usually encompass more than one terrestrial biome. This is also the case of the "pampean" river basins, which, in addition to the grassland Pampa, include parts of the Atlantic Forest in their upper portions.

We used Freshwater Ecoregions of the World (FEOW; Abell et al. 2008) as a framework to provide a preliminary notion of fish species richness in the Brazilian and Uruguayan Pampa in comparison to species richness in other South American regions. We geographically defined the pampean ecoregions by intersecting the Pampa grasslands (Fig. 12.1) with the freshwater ecoregions (Fig. 12.2) in order to account only for species occurring in pampean portions of the freshwater ecoregions. Fish richness data for other South American ecoregions were taken from Albert et al. (2011), and species density (species richness scaled to geographical area) was calculated as C = number of species/$A^{0.3348}$, where A is the geographical area and 0.3348 is the scaling exponent of the species-area relationship for South American freshwater fishes, as estimated by Albert et al. (2011).

With a total of 334 freshwater fish species across three freshwater ecoregions (Table 12.1), the Pampa has a relatively high species richness and species density in comparison to other South American regions (Fig. 12.9).

In the Pampa, mean fish species richness by ecoregion, considering the three freshwater ecoregions, is generally lower than in Amazonian ecoregions and similar to coastal Atlantic and Parana ecoregions. However, if the sum of all species in the Pampa is considered (Fig. 12.1, dashed lines), both richness and species density are comparable to Amazonian ecoregions and higher than other ecoregions. This high diversity possibly results from the relatively low proportion of species shared among pampean ecoregions, since only 27.7% species are shared between pampean

Table 12.1 Freshwater fish diversity in the Pampa north of the Río de La Plata. Species numbers considered valid species compiled up to 2023

	Freshwater ecoregions[a]			Pampa
	Lower Uruguay[b]	Laguna dos Patos[c]	Tramandaí-Mampituba[c]	
Number of species	252	151	72	334
Species density	3.83	2,90	6.92	4.43
Area (km^2)[d]	270,456	134,507	1092	406,054

[a] Freshwater ecoregions intersecting the Pampa north of the Río de La Plata

[b] Species that occur in the pampean areas of freshwater ecoregions (FEOW) north of the Río de La Plata

[c] Not including species that occur only in the Atlantic Forest section of this ecoregion

[d] LU according to Abell et al. (2008); LP area in the Pampa only; TM area defined by the coastal plain territory within the Tramandaí river watershed

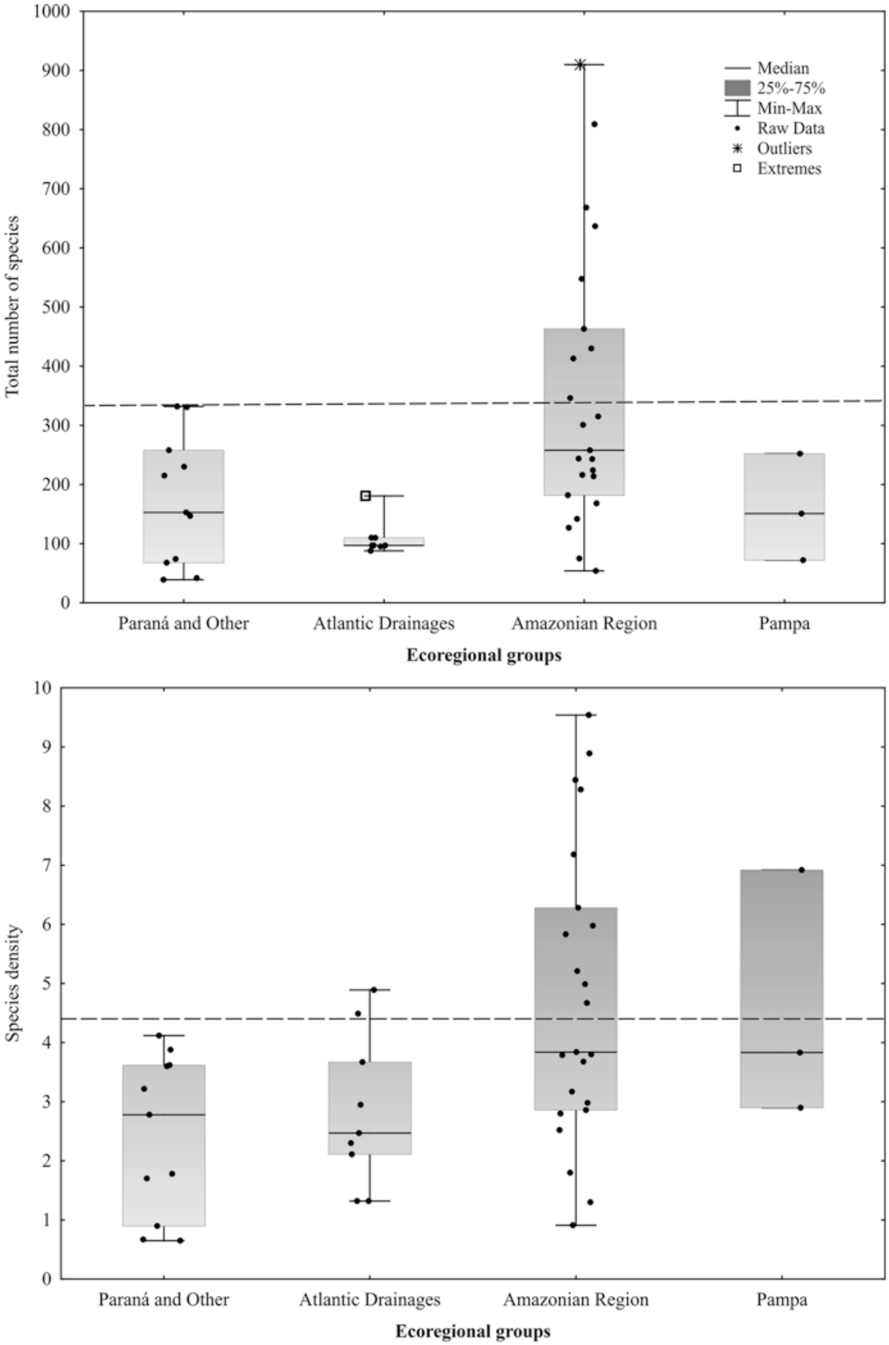

Fig. 12.9 Mean fish species richness (above) and fish species density (below) in different groups of freshwater ecoregions of South America. Species density calculated according to Albert et al. (2011; see text). Data on species number and species density for 44 Neotropical freshwater ecoregions (FEOW) were extracted from Albert et al. (2011; Table 12.1), except for ecoregions intersecting the Pampa (see main text), which are updated here. Area (km^2) was estimated only for the pampean portions of these FEOW. Note that species data in Albert et al. (2011) were compiled in 2008, while our data for the Pampa is updated to 2023. Dashed lines represent pooled values for the whole Pampa

Table 12.2 Freshwater fish species in grassland ecosystems of southern Brazil and Uruguay. Highland grasslands include the *Campos do Paraná* (in the state of Paraná) and the *Campos de Cima da Serra* (in the states of Santa Catarina and Rio Grande do Sul)

	Pampa	Highland grasslands of southern Brazil		*Campos Sulinos* (BR, UY)
		Campos do Paraná	*Campos de cima da serra* (RS, SC)	
Number of species	334	149 (32)[a]	82 (31)[a]	570 (334)[a]
Number of endemics (%)[b]	102[c] (30.5%)	*[d]	18	117

[a] Pampean species in brackets

[b] Species known to occur only within the Pampa limits (% of total number of pampean species in the respective freshwater ecoregions – FEOW)

[c] Includes 24 endemic pampean species shared between two or more FEOW

[d] Data not available

freshwater ecoregions, while 72.3% are unique to only one freshwater ecoregion (Fig. 12.2).

In comparison to the Pampa, aquatic ecosystems in the highland grasslands of southern Brazil are somewhat poorer in fish species, but have a higher proportion of endemics (Table 12.2). This higher endemism is possibly a result of the geographic isolation of these areas, which are located in the headwaters of different river basins, as exemplified by the endemic species of *Cambeva* (Trichomycteridae) and *Eurycheilichthys* (Loricariidae).

12.5 Environmental Pressure on Fish and their Habitats

Freshwater fishes in the Pampa are under pressure from multiple and overlapping factors: land use (including land cover conversion to agriculture, forestry, and urban areas), damming, mining, road network, invasive species, and fisheries. In the Brazilian Pampa, more than 50% of the small to medium watersheds (Strahler order 2 to 3) are under intermediary to high environmental pressure (Meneses 2016), mainly due to natural vegetation being converted to agriculture and forestry, and also due to livestock use. Loss of watershed and riparian integrity in pampean streams affects size structure of fish communities (Benejam et al. 2016; Pott et al. 2021), and fish functional and taxonomic diversity (Chalar et al. 2013; Dala-Corte et al. 2016, 2017, 2019; Mello 2017; Moi and Teixeira-de-Melo 2022), resulting in local extinctions (Zarucki et al. 2011; Camana et al. 2020).

Agriculture, urbanization, and livestock grazing heavily affect the ephemeral wetlands inhabited by several endangered annual fish species (Rivulidae) (Volcan et al. 2015; Loureiro and Bessonart 2017), which correspond to about 60% of all threatened fish species in the Brazilian Pampa. Furthermore, in the Uruguayan Pampa, evidence for the presence of sublethal concentrations and bioaccumulation of pesticides in migratory and non-migratory fish of commercial value (e.g., *Hoplias*

Table 12.3 Weirs and reservoirs in the Brazilian Pampa. Numbers were extracted from a regional 1:25.000 digital cartographic database. (SEMA 2018)

Area	*N*	%
<10 ha	21,920	82.9
10 a 100 ha	4173	15.8
100 a 1000 ha	331	1.3
1000 a 10,000	5	<0.1
>10,000 ha	2	<0.1
Total	26,431	

argentinensis) is increasing (Ernst et al. 2018; Soutullo et al. 2020), as well as the presence of microplastics (Vidal et al. 2021) and human pharmaceuticals (Rojo et al. 2019).

Weirs and reservoirs are also a potential pressing factor. There is a large number of weirs and reservoirs (>26.000) spread across the Brazilian Pampa (Table 12.3), most of which are smaller than 10 hectares. These reservoirs either fragment watercourses or manage water for agriculture and urban supply. Such a high number of reservoirs has the potential for large cumulative impacts (yet to be assessed in the Pampa) on the natural flow regime and hydrological conditions of streams and wetlands, which are essential properties of the dynamic habitats of freshwater fishes (see Morden et al. 2022). For example, stream flow can be reduced to a degree where fish survival is no longer possible, at least temporarily, which can lead to a reduction in the abundance and reproductive output, increasing the risk of local extinctions. This impact can be severe in wetlands under the influence of dams built for agricultural use, where several endangered annual fish (Rivulidae; Cyprinodontiformes) occur, and for which local extinction would also mean global extinction. Not many large and mid-sized rivers have been dammed in the Brazilian Pampa, but fragmentation of the main migratory fish routes has been caused by dams outside the Brazilian Pampa (Salto Grande Dam, in lower Uruguay river; Palmar, Baygorria, and Rincón del Bonete in the Negro river; Itá dam and Foz do Chapecó, in the upper Uruguay river, and the Ijuí river). A striking example is the Negro river (the largest tributary of lower Uruguay river), where at least the larger migratory species such as *Salminus brasiliensis*, *Prochilodus lineatus*, *Megaleporinus obstusidens*, and *Pseudoplatystoma corruscans* have been wiped out from 80% of the basin (Serra et al. 2014). Another example of local extinction is the case of *Piaractus mesopotamicus* from the lower Uruguay river. This species was relatively common before the construction of the Salto Grande Dam (Devincenzi and Teague 1942; Sierra et al. 1977) but disappeared after the closure of the dam.

Furthermore, in the lower Uruguay river basin, an unfortunate synergy between reservoirs and agriculture eutrophication has been recently documented. These factors are increasing the presence and toxicity of cyanobacterial blooms (de la Escalera et al. 2023; Kruk et al. 2023), with so far unknown consequences for fish populations. Agricultural activities also influence pampean stream ecosystems through the input of herbicides and pesticides, which should be a matter of concern given the accelerated rate of grassland conversion to agriculture in the last 20 years (Baeza et al. 2022). Several studies have shown the impacts of herbicides and pesticides on pampean freshwater ecosystems and their fish (e.g., Glusczak et al. 2006; Griffero et al. 2019; Iturburu et al. 2019; Bergmann et al. 2020; Marins et al. 2020; Storck et al. 2022).

Mining is currently a pressing factor in several pampean watersheds. Various mining products, including coal, oil shale, zinc, copper, lead, titanium, phosphate, gemstone mining, granite, quartzite, sand, arenite, clay etc. are currently explored or have the potential for exploration in the region (SME/RS 2018; SPGG/RS 2020). Mining affects fish and their habitats in several ways, e.g., changing hydrology, increasing sediment input and overburden of stream channels, decreasing water quality (e.g., low pH and contamination with heavy metals and other toxic substances). These alterations result in other ecosystem changes that ultimately will also affect fish (Daniel et al. 2015; Azevedo-Santos et al. 2021). Although specific assessments of mining impacts on pampean fishes are rare (e.g., Bruschi et al. 2000; Fontoura et al. 2021), mining is known to have high negative effects on fishes, both locally and regionally (Daniel et al. 2015). Sand mining is particularly common in the lower course of several pampean rivers and should be closely regulated by environmental agencies due to its potential for habitat degradation and systemic effects. Several directions for environmental regulation and control of sand mining in the Guaíba Lake (Laguna dos Patos basin) have been proposed after a comprehensive assessment of fish distribution (Fontoura et al. 2021). However, the effects of sand mining on fish and their habitats remain largely unassessed in other areas.

Roads can negatively affect streams and fishes (Angermeier et al. 2004), and their impacts on freshwaters of the Pampa are potentially high in some regions (Flores et al. in press), particularly when affecting restricted range lowland species such as rivulids (Volcan et al. 2015) or in synergy with land use and catchment hydrology alteration. In more than half landscape units of the Laguna dos Patos and Tramandaí-Mampituba ecoregions, streams are under intermediate to high environmental pressure from roads (Flores et al. in press).

Fisheries possibly act in combination with other factors (land use, damming) to affect fish populations, particularly of migratory or large-sized species in the main stem of large rivers such as the Uruguay, Ibicuí, and Negro rivers. In Brazil, except for fragmentary data and episodic scientific research (e.g., Milani and Fontoura 2007; Ceni et al. 2016), there is a general lack of systematic monitoring and assessment of freshwater fisheries in the region, and a long-term program of fisheries monitoring by official agencies is urgently needed. In the Uruguayan and Argentinean sectors of the Uruguay river, CARU (Comisión Admnistradora del Río Uruguay) conducts some evaluation of the artisanal fisheries pressure on fish stocks. In fact, for several species there are some size limitations and seasonal bans for the catches (*Prochilodus lineatus*, *Salminus brasiliensis*, *Ageneiosus inermis*, *Pimelodus maculatus*, *Pseudoplatystoma corruscans*, *Luciopimelodus pati*, and *Odontesthes* spp.). Furthermore, the capture of certain species is not allowed (*Brycon orbignyanus*, *Oxydoras kneri*, *Pseudoplatystoma reticulatum*).

12.6 Non-native and Invasive Species

There are at least 13 non-native (non-Neotropical) fish species in freshwaters of the Pampa and the highland grasslands of southern Brazil (Table 12.4). They have mostly been introduced for fish culture and subsequently escaped to open habitats (rivers, streams, lakes and reservoirs), except the black-bass, *Micropterus salmoides*, and rainbow-trout, *Oncorhynchus mykiss*, which have been introduced for

Table 12.4 Non-native freshwater fish species in grassland ecosystems of southern Brazil and Uruguay

	HG	Pampa			
Species		TM	LP	LU	UU
Acipenseriformes					
Acipenseridae					
Acipenser baerii Brandt 1869	0	0	0	1	0
Acipenser gueldenstaedtii Brandt & Ratzeburg 1833	0	0	1	1	0
Acipenser ruthenus Linnaeus 1758	0	0	0	1	0
Centrarchiformes					
Centrarchidae					
Micropterus salmoides (Lacepède, 1802)	1	0	1	1	1
Cichliformes					
Cichlidae					
Coptodon rendalli (Boulenger, 1897)	0	1	1	1	1
Oreochromis niloticus (Linnaeus, 1758)	1	1	1	1	1
Cypriniformes					
Cyprinidae					
Cyprinus carpio Linnaeus, 1758	1	1	1	1	1
Xenocyprididae					
Ctenopharyngodon idella (Valenciennes, 1844)	0	0	1	1	0
Hypophthalmichthys molitrix (Valenciennes, 1844)	0	1	1	1	0
Hypophthalmichthys nobilis (Richardson, 1845)	0	1	1	1	0
Salmoniformes					
Salmonidae					
Oncorhynchus mykiss (Walbaum, 1792)	1	0	1	0	1
Siluriformes					
Clariidae					
Clarias gariepinus (Burchell, 1822)	0	0	1	0	0
Ictaluridae					
Ictalurus punctatus (Rafinesque, 1818)	1	0	1	0	1
Total	5	5	11	10	6

Species presence in a given region does not mean it is widespread, only that it has been recorded in at least one open habitat location in the region

HG highland grassland watersheds. Pampean freshwater ecoregions north of the La Plata river: *TM* Tramandaí-Mampituba, *LP* Laguna dos Patos, *LU* Lower Uruguay river, *UU* Upper Uruguay river

1 = presence; 0 = absence

sport-fishing. Fish stocking in rivers and reservoirs is another cause of non-native fish introduction, despite being illegal in both countries, with carps and tilapias often released in rivers and reservoirs. The impacts of these introductions on native species and ecosystems can be potentially severe, as documented in the literature (see reviews in Britton 2022; Rocha et al. 2023). Reductions in species richness, biomass and abundance have been associated with stocking of rainbow trout in highland streams (Winckler-Sosinski et al. 2009). Another study comparing freshwater fish diversity in several small ponds (*açudes*) in the Pampa showed that in ponds with a long existence (about 30 years) of *Micropterus salmoides*, none to a maximum of three native species cohabited (*Geophagus brasiliensis*, *Astyanax laticeps* and *Synbranchus marmoratus*), the populations of most native species being eliminated or greatly reduced (Carvalho et al. 2012). However, for most other non-Neotropical species, impacts have not yet been properly assessed in the Pampa or in the highland grasslands (as well as in other parts of Brazil; Rocha et al. 2023). Published studies usually only document the presence of non-native species (e.g. Braun et al. 2003; Machado et al. 2015; Chuctaya et al. 2019; Zarucki et al. 2021) or assess the risk of invasion (Troca and Vieira 2012).

Apart from non-Neotropical species introductions, fish invasions by inter-basin dispersion have also occurred in the Pampa. These invasions primarily involve species native to the Uruguay river basin (and occasionally the Paraná river basin), which are now found in the Laguna dos Patos and Tramandaí-Mampituba freshwater ecoregions (Table 12.5). All of these species were unintentionally introduced, except *Hoplias lacerdae,* introduced for fish culture. They likely dispersed from the Lower Uruguay ecoregion basin to the other pampean ecoregions through man-made channels opened for agricultural water management (Bertaco et al. 2022). Four of these species are now relatively widespread and abundant in the invaded ecoregions, mainly in rivers, lakes and wetlands (Loureiro et al. 2020; Bertaco et al. 2022; Bertaco and Azevedo 2023): *Acestrorhynchus pantaneiro*, *Pachyurus bonariensis, Serrasalmus maculatus*, and *Trachelyopterus lucenai*. Other species (*A. anisitsi, C. spilotus, S. brevipinna, P. iheringi*, Table 12.5) were only rarely recorded. Interestingly, non-native fish species (either exotic or Neotropical inter-basin invaders) are absent or at least rare in low order non-urban pampean streams, as suggested by data from several sites (Teixeira-de Mello et al. 2012; Dala-Corte et al. 2016). This situation contrasts with some other regions in Brazil where fish invasions in streams have been much more pervasive (Magalhães et al. 2021; Santos et al. 2023).

Apart from non-native fish, a significant aquatic invader affecting native fishes is the golden mussel (*Limnoperna fortunei*). In the La Plata basin, its invasion is estimated to have begun in the 1990s (Pastorino et al. 1993) and has changed the trophic web in the lower Uruguay river. This hypothesis has received recent support from the findings of González-Bergonzoni et al. (2023). In their study, they employed a combination of gut content analysis, stable isotopes, and gut morphometry to examine both recently collected fishes and historical museum lots, having found a reduction in diet diversity and an increase in the trophic position of two omnivorous species (*Megaleporinus obtusidens* and *Pimelodus maculatus*).

Table 12.5 Neotropical non-native freshwater fish species in pampean freshwater ecoregions north of the Río de La Plata

Species	Invasive range
Characiformes	
Acestrorhynchidae	
Acestrorhynchus pantaneiro Menezes, 1992	LP, TM
Characidae	
Aphyocharax anisitsi Eigenmann & Kennedy, 1903	LP, TM
Curimatidae	
Cyphocharax spilotus (Vari, 1987)	LP, TM
Steindachnerina brevipinna (Eigenmann & Eigenmann 1889)	LP
Erythrinidae	
Hoplerythrinus unitaeniatus (Spix & Agassiz, 1829)	LP
Hoplias lacerdae Miranda-Ribeiro, 1980	LP
Serrasalmidae	
Serrasalmus maculatus Kner, 1858	LP
Perciformes	
Sciaenidae	
Pachyurus bonariensis Steindachner, 1879	LP
Siluriformes	
Aspredinidae	
Pseudobunocephalus iheringii (Boulenger, 1891)	TM
Auchenipteridae	
Trachelyopterus lucenai Bertoletti, da Silva & Pereira, 1995	LP, TM

Most of these species are native to the Uruguay river basin and have invaded the Laguna dos Patos (LP) and Tramandaí-Mampituba (TM) freshwater ecoregions. Species presence in a given region does not mean it is widespread, only that it has been recorded in at least one open habitat location in the region

12.7 Threatened Species

Conservation strategies for fishes in the Brazilian Pampa are largely insufficient or weakly implemented, being restricted to extinction risk assessments and action plans targeted at a few annual fish species. Nevertheless, extinction risk assessments are a very important conservation tool and have been used as a reference for environmental licensing decisions and for planning purposes by regional environmental agencies (e.g. Becker et al. 2017, Ferraro and Anele 2022). A regional (i.e., Rio Grande do Sul) official red list has been prepared in 2003 (Fontana et al. 2003) and reviewed in 2014 (Rio Grande do Sul 2014). In Brazil, the assessment of extinction risk for all Brazilian vertebrates was recently updated (MMA 2022), whereas the IUCN maintains a continuous effort to evaluate all species on Earth (IUCN 2023). In the Uruguayan Pampa, conservation actions are also insufficient and there is only a list of priority species for conservation by the National Protected Areas System (Loureiro et al. 2013), but no specific protection policies. Considering the existing red lists, there are 47 species of fish threatened with extinction in the Pampa, most of which are rivulids (27 species) (Table 12.6). Annual fish (Rivulidae) are the only

Table 12.6 Threatened fish species in the Pampa and highland grasslands of southern Brazil

Family/species	Category	Source	Distribution
Crenuchidae			
Characidium vestigipinne	CR	MMA/IUCN	UPG-BR
Bryconidae			
Brycon orbignyanus	CR	MMA	RPG-BR/AR/UY*
Salminus brasiliensis	VU/EN	Rio Grande do Sul (2014)	RPG-BR/AR/UY*
Characidae			
Astyanax eremus	CR	MMA/IUCN	UPG-BR
Diapoma pyrrhopteryx	EN	MMA/IUCN	UPG-BR
Trichomycteridae			
Cambeva crassicaudata	EN	MMA/IUCN	UPG-BR
Cambeva igobi	VU/EN	MMA/IUCN	UPG-BR
Cambeva mboycy	EN	MMA/IUCN	UPG-BR
Cambeva pascuali	CR/VU	MMA/IUCN	UPG-BR
Cambeva tropeiro	CR/EN	MMA/IUCN	UPG-BR
Loricariidae			
Isbrueckerichthys saxicola	EN/CR	MMA/IUCN	UPG-BR
Pogonopoma obscurum	EN/VU	MMA/IUCN	UPG-BR
Pimelodidae			
Pseudoplatystoma corruscans	VU	MMA	RPG-BR/AR/UY*
Steindachneridion melanodermatum	EN	MMA/IUCN	UPG-BR/AR
Steindachneridion scriptum	EN	MMA	RPG-BR/AR/UY
Cichlidae			
Crenicichla empheres	VU	MMA/IUCN	UPG-BR
Crenicichla hadrostigma	VU	MMA/IUCN	UPG-BR/AR
Atherinopsidae			
Odontesthes bicudo	EN	MMA/IUCN	RPG-BR
Rivulidae			
Austrolebias adloffi	EN	MMA/IUCN	RPG-BR
Austrolebias affinis	VU	IUCN	RPG-UY
Austrolebias alexandri	EN	MMA	RPG-BR/AR/UY
Austrolebias arachan	VU	MMA	RPG-BR/UY
Austrolebias bagual	CR	MMA/IUCN	RPG-BR
Austrolebias camaquensis	EN	MMA/IUCN	RPG-BR
Austrolebias cheradophilus	CR	MMA	RPG-BR/UY
Austrolebias cinereus	CR	MMA/IUCN	RPG-BR/UY
Austrolebias cyaneus	EN	MMA	RPG-BR
Austrolebias elongatus	EN	IUCN	RPG-AR/UY
Austrolebias gymnoventris	EN	IUCN	RPG-BR/UY

(continued)

Table 12.6 (continued)

Family/species	Category	Source	Distribution
Austrolebias ibicuiensis	EN	MMA	RPG-BR
Austrolebias jaegari	EN	MMA	RPG-BR
Austrolebias litzi	VU	MMA	RPG-BR
Austrolebias nachtigalli	VU	MMA	RPG-BR
Austrolebias nigrofasciatus	EN	MMA/IUCN	RPG-BR
Austrolebias paucisquama	VU	MMA	RPG-BR
Austrolebias pelotapes	EM/CR	MMA/IUCN	RPG-BR
Austrolebias pongondo	EN	MMA	RPG-BR
Austrolebias queguay	CR	IUCN	RPG-UY
Austrolebias quirogai	CR/EN	MMA/IUCN	RPG-BR/UY
Austrolebias reicherti	EN	IUCN	RPG-BR/UY
Austrolebias univentripinnis	CR	MMA	RPG-BR/UY
Austrolebias varzeae	CR/VU	MMA/IUCN	UPG-BR
Austrolebias viarius	EN	IUCN	RPG-UY
Cynopoecilus intimus	VU	MMA/IUCN	RPG-BR
Cynopoecilus notabilis	LC/VU	MMA/IUCN	RPG-BR
Poeciliidae			
Cnesterodon holopteros	EN	IUCN	RPG-UY
Cnesterodon omorgmatos	CR	MMA/IUCN	RPG-UY

See main text for sources. Asterisk indicates species with broader distributions
UPG upland grasslands or *campos de altitude*, *RPG* lowland grasslands in the Pampa or *Pastizales del Río de La Plata*

group for which management plans are underway (ICMBio 2013, 2022; SEMA 2021), and listing of migratory species is under constant debate because of implications for fisheries. The number of threatened pampean fish species is possibly underestimated, since extinction risk assessments of many pampean species are greatly affected by lack of data and specialists, while environmental pressure in many areas is significant, as described previously.

12.8 Protected Areas in the Brazilian and Uruguayan Pampa

Increasing the area of freshwater protected habitats and their representativeness for the pampean fish species (particularly threatened and endemic species) must be an important consideration for regional conservation strategies. In terms of freshwater habitats, protected areas in the Pampa provide only 0 to 2.5% of effective protection to lentic and lotic habitats, depending on the aquatic ecoregion (MVOTMA 2015, Jacobi et al. in press), and are thus far from reaching the international targets (30% of terrestrial and aquatic ecosystems; CBD 2022).

In the Brazilian Pampa, the number of protected areas is limited (n = 32[1]) and typically too small for reasonably protecting fish populations. Specifically, there are only four protected areas with total surfaces larger than 100 km^2 (Parque Estadual do Camaquã, 101.67 km^2; Parque Estadual Delta do Jacuí, 141.82 km^2; Parque Nacional da Lagoa do Peixe, 324.94 km^2; Estação Ecológica do Taim, 328.05 km^2), all of them in lowlands of the Laguna dos Patos ecoregion. Therefore, in addition to the small areal coverage, the representation of different aquatic habitats and distinct pampean ecoregions is unbalanced in the protected area system. Large wetlands are relatively well covered by protected areas in the coastal plain (Burger and Ramos 2007) and Laguna dos Patos ecoregion. However, streams, rivers, floodplains, coastal lakes (Serra et al. 2014; Jacobi et al. in press) and temporary wetlands are largely underrepresented. In Uruguay, two areas of this ecoregion are representative of fast flowing waters (aprox. 450 km^2) (Paisaje Protegido Paso Centurión y Sierra de Ríos and Paisaje Protegido Quebrada de los Cuervos y Sierras del Yerbal), while four others cover mainly wetlands, freshwater and coastal environments (aprox. 800 km^2) (Paisaje Protegido Laguna de Castillos, Paisaje Protegido Laguna de Rocha, Parque Nacional San Miguel, and Área de Manejo de Hábitats y/o Especies Laguna Garzón).

The Lower Uruguay ecoregion and the pampean portions of the Upper Uruguay and Tramandaí-Mampituba ecoregions are also poorly represented in the protected area system. In Uruguay, there are four protected areas in the lower Uruguay, with a combined area of approximately of 600 km^2, two of which in wetlands associated with the Uruguay river (Parque Nacional Esteros de Farrapos e Islas del Río Uruguay and Área de Manejo de Hábitats y Especies Rincón de Franquía), one including wetlands and lotic environments of the Queguay river (Área Protegida con Recursos Manejados Montes del Queguay), and one associated exclusively with fast flowing streams (Paisaje Protegido Valle del Lunarejo).

Only about 25% of the threatened fish species of the Pampa have been recorded in protected areas (Jacobi et al. in press), highlighting the need to increase the network of areas under formal protection. The lack of protection affects not only migratory species that require both large areas and complex conservation strategies (Bailly et al. 2021), but also annual fish species with very restricted geographic distributions (Volcan et al. 2015), which would require relatively small conservation areas. Furthermore, many freshwater species (particularly migratory taxa) depend on areas that go beyond national boundaries, although integrated international conservation policies (including protected areas) have not been implemented so far (CIC 2017).

Another important tool for conservation policies in Brazil is the definition of priority areas for the conservation of fish and freshwater habitats. Priority areas not only guide the selection of new areas to be added to the national system of protected areas, but also set spatial priorities for conservation initiatives in private lands, for

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[1] We excluded four areas of the category "APA – Environmental Protection Area", because they are very large but have low effectiveness for protecting aquatic habitats.

public environmental policies and for allocation of resources to environmental control and management. Priority areas have been officially defined for the Brazilian Pampa (MMA 2018).

Habitat restoration is probably a necessary target in areas where land use change has severely affected watershed or riparian integrity (Dala-Corte et al. 2016; Meneses 2016) or where connectivity and hydrological regime is under influence of small dams (Table 12.2) and road crossings (Flores et al. in press). However, to our knowledge, there is no large-scale public policy for watershed, stream or wetland restoration in the Pampa region, in spite of the large loss of wetland areas and their connectivity.

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Chapter 13
Wetlands in the *Campos Sulinos*: Diversity, Functions, and Threats

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13.1 Introduction

Wetlands are among the most productive ecosystems on the earth, with enormous ecological and social importance. Wetlands in their natural state provide substantial benefits to the sustainability of a region (Batzer and Sharitz 2014). Water storage and purification, flood protection, aquifer recharge, grain production, energy and recreation are some of the various functions these ecosystems provide for humanity. Costanza et al. (2014) estimated that services and goods provided per unit area of wetlands (US\$14,785 ha^{-1} $year^{-1}$) exceed the values provided by the world's forests (US\$232 ha^{-1} $year^{-1}$).

Wetlands are ecosystems of high biological diversity (Batzer and Sharitz 2014). Estimates indicate that 10% of the identified species of the planet (130,000 species) occur in continental wetlands, although these habitats cover less than 1% of the earth's surface (Dijkstra et al. 2014). Such high species diversity is a consequence of the different wetland types that exist in the world, from marine to coastal to continental, including the human-made ones (Cowardin et al. 1979). Furthermore,

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habitat variations such as depth, aquatic plant types, size, and hydroperiod also contribute to the high species diversity of these ecosystems (Guadagnin and Maltchik 2007; Rolon and Maltchik 2006; Stenert and Maltchik 2007).

The diversity of wetland types makes it difficult to develop a single definition that encompasses all wetland ecosystems (Maltchik et al. 2018). Therefore, researchers suggest that the basic definition of wetlands is related to their key attributes: presence of water, hydromorphic soils, and water-adapted biota (Cowardin et al. 1979). In Brazil, Junk et al. (2014) proposed a definition based on those attributes. In addition, the authors proposed the first hierarchical classification of Brazilian wetlands. This classification holds as a key element the fluctuation of the water level, which essentially discriminates the large wetlands of the Amazon and Pantanal from the small-sized ones of the southern region of Brazil (of the South region). Despite their small surface areas, southern Brazilian wetlands provide similar ecosystem functions and services as the large, tropical wetlands. Indeed, global meta-analysis covering over 300 wetlands across 51 countries indicated that small wetlands provide a greater range of ecosystem services than large wetlands (Chaikumbung et al. 2016).

In southern Brazil (Rio Grande do Sul state), most wetlands are small-sized, although accurate inventories are lacking. Maltchik et al. (2003) identified 3441 wetlands across the state, and approximately 40% of inventoried wetlands had surface areas smaller than 5 ha (Maltchik et al. 2003). Across the *Campos Sulinos*, the general characteristics of the wetlands strongly vary between the Atlantic Forest and Pampa regions (“biomes” according to IBGE 2019) that comprise this region. In the Atlantic Forest (highland grasslands), wetlands are smaller, shallower, more isolated, mostly temporary, and with more than one dry period over a year (Knauth et al. 2018; Pires et al. 2018). In the Pampa (Pampa grasslands), wetlands are larger, deeper, non-isolated, with a strong reduction of surface water in summer and – when intermittent – with only one drought per year (Knauth et al. 2019; Bertuzzi et al. 2019; Bacca et al. 2021). Species diversity of several taxa is high in wetlands across both regions.

Despite their high biological diversity and the multitude of ecosystem services provided, wetlands in the *Campos Sulinos* are strongly threatened. Although detailed data on wetland loss are scarce, earlier estimates suggested that over 90% of the existing wetlands are either lost to or impacted by anthropogenic activities, especially conversion to agriculture (rice fields), urban areas, and tree plantations (Maltchik et al. 2003). Rice fields have a strong impact on the diversity and community structure of many wetland species, e.g., invertebrates, plants, tadpoles, and waterbirds (Moreira et al. 2016; Maltchik et al. 2017), and so do pine plantations (Rolon et al. 2011; Stenert et al. 2012). In terms of conservation, this situation is difficult to reverse due to the economic importance of both activities in the region. The state of Rio Grande do Sul contributes with over 65% of the total Brazilian rice production, while forestry activities have been strongly sponsored since the 1960s and remain in expansion in the region (see Ribeiro et al. 2020). However, the overall number of protected areas in the *Campos Sulinos* is low (less than 3% in the case of the Pampa), and even smaller when wetland protection is considered. Currently, two

Ramsar wetland sites are legally protected by Brazilian environmental laws in the Pampa grasslands: Lagoa do Peixe National Park and Taim Biological Station. Both Ramsar sites are of enormous importance to the aquatic biodiversity of the Pampa grasslands, especially endemic and migratory waterbird species. Ribeiro et al. (2020) showed that the inner areas of both Ramsar sites are well conserved in terms of natural cover and are currently not much subjected to anthropogenic pressures.

In this chapter, we cover most of the recent knowledge produced in relation to the wetland ecosystems of Pampa and South Brazilian highland grasslands, i.e., the *Campos Sulinos* region. We review the main drivers of the biodiversity of small wetlands; the contribution of specific land-management practices to wetland-dependent wildlife; the importance of dispersal processes to the biodiversity of isolated wetlands; the occurrence of endemic and endangered annual fish species; and the importance of restoration initiatives in impacted wetlands. Finally, we provide some suggestions that provide relevant information to wetland conservation and management in the *Campos Sulinos*.

13.2 Drivers of the Biodiversity of Small Wetlands and Wetland-Dependent Wildlife: The Hydroperiod Leads, but Space and Traits Also Matter

Considering the threatened wetland status in the *Campos Sulinos* (Maltchik et al. 2003), understanding of the drivers of the biodiversity of the wetland-dependent wildlife is crucial to conservation policies in the region. The knowledge of the drivers of such high wetland biodiversity is incipient. This is because most previous research works on wetland species diversity are limited to inventories of specific taxa that either cover the range of the state of Rio Grande do Sul (RS) (Maltchik et al. 2009, 2010) or are embedded within biodiversity reviews of specific subregions (Becker et al. 2006; Bond-Buckup 2008). Studies that address the biodiversity drivers and the ecological dynamics of the small-wetland biota in the *Campos Sulinos* are more recent.

Hydroperiod (i.e., the length of the wet phase) is the main driver of wetland biodiversity (Dodds and Whiles 2020). The differences in local species composition commonly observed between permanent and temporary wetlands is attributed both to the role of drought (that filters out species unable to cope with dry periods) and to the varying environmental conditions (e.g., habitat structure, water chemistry) and biotic interactions (e.g., predation rates) that occur in wetlands along different hydroperiods (Wellborn et al. 1996). The climate in southern Brazil is characterized by hot summers. Surface water of smaller wetlands tends to totally or partially disappear in the warmer periods of the year, and thus most freshwater wetlands alternate flooded (usually from fall to spring) and dry periods (summer). This creates a mosaic of temporary wetlands with different hydroperiods coexisting with larger, permanent wetlands across the landscape (Maltchik et al. 2004). In accordance with the general expected pattern, earlier space-for-time studies evidenced that the taxonomic composition of multiple taxa (e.g., algae, macroinvertebrates, plants) differed between temporary and permanent wetlands (Maltchik et al. 2010; Rolon and Maltchik 2006; Stenert and Maltchik 2007). Nevertheless, beyond the coarse comparison between temporary and permanent hydroperiods, it has been increasingly recognized that biodiversity patterns in temporary wetlands can vary according to more fine-grained changes in hydroperiod. In specific, temporary wetlands differ in relation to various hydrological aspects, e.g., the number of dry and wet months, inundation timing, and filling rates. Subtle variations in those aspects of the hydrological regime can lead to important changes in wetland biodiversity (Jeffries et al. 2016).

In the highland grassland region, wetland habitats vary according to the lengths of their flooded periods, onset of their wet phases, and filling rates, leading to a landscape composed of short- to long-hydroperiod (i.e., permanent) wetlands (Pires et al. 2021) (Fig. 13.1a). Recent studies showed that such differences in hydroperiod length were important drivers of the richness and composition of animal communities in the region (Knauth et al. 2018; Pires et al. 2021; Stenert et al. 2017). Specifically, higher diversity of microcrustacean assemblages (Cladocera) hatching was detected in the sediment of medium- and short-hydroperiod wetlands compared to long-hydroperiod ones, suggesting that reduced hydroperiods stimulated the production of dormant stages (Stenert et al. 2017). Long-hydroperiod wetlands supported higher richness of dragonfly larvae (Odonata, Insecta), while larvae with life-history traits related to survival to dry periods (e.g., Lestidae) were more common in shorter hydroperiods (Pires et al. 2019).

There was also strong spatial and seasonal variation in the local environmental conditions (e.g., vegetation structure, water chemistry) and predator presence among hydroperiods (Pires et al. 2021). The hydroperiod gradient thus likely drove the strength of biotic interactions that underlie the observed patterns in assemblage structure of wetland invertebrate and vertebrate taxa in highland grasslands. For instance, the complexity of the surrounding vegetation was directly associated with longer hydroperiods and explained the higher diversity of spider assemblages in wetlands with more complex habitat structure (Ávila et al. 2017). Fish presence also co-varied with hydroperiod (fishes were absent in reduced hydroperiods). The potential stronger predation pressure exerted by fishes was suggested as the driver

Fig. 13.1 (**a**) Small temporary wetland in the highland grassland region; (**b**) wetlands in the Pampa region; and (**c**) wetland fragmented by rice field expansion. (Photos: Leonardo Maltchik)

of the lower tadpole richness found in the long-hydroperiod wetlands (Knauth et al. 2018) as well as the distinct taxonomic and functional compositions of macroinvertebrates reported between fish and fishless wetlands (Boelter et al. 2018). Finally, there is strong evidence that changes in hydroperiod length interfered in the metacommunity dynamics of aquatic taxa in the region. Spatial location and environmental variables had varying influences on the composition of aquatic macroinvertebrates in each hydroperiod over the seasons: while environmental variables explained the overall metacommunity structure in colder seasons, spatial variables prevailed in the spring. However, active- and passive-dispersing macroinvertebrates were distinctly influenced by spatial and environmental variables in each season. This suggests that hydroperiod length differently affects the metacommunity dynamics of passive- and active-dispersing macroinvertebrates (Pires et al. 2021).

In the Pampa grasslands, a region warmer and less humid than the highland grasslands, small wetlands coexist with much larger remaining wetland fragments (Junk et al. 2014) (Fig. 13.1b). In the coastal region of the Pampa, previous studies showed that intermittent dune wetlands supported lower richness and distinct composition of macroinvertebrate and macrophyte taxa compared to permanent ones. Specifically, permanent wetlands supported a higher proportion of predatory macroinvertebrate taxa and hydrophyte species, while no species discriminated the intermittent wetlands (Rolon et al. 2008; Stenert and Maltchik 2007). This suggests that wetlands with longer hydroperiods favor the occurrence of long-living species with adaptations to wet conditions, while taxa inhabiting intermittent wetlands also occur in permanent ones. Wetland hydroperiod was also important to explain anuran distribution in the Pampa. Although richness and composition of adult and tadpole anurans also differ between temporary and permanent wetlands, again, as in the case of the highland grassland wetlands, incorporating finer-grained information on hydrological aspects of wetlands highlights a more complex scenario of biodiversity structuring (Moreira et al. 2010). Specifically, the number of dry months was an important predictor of anuran composition and adult abundance; permanent and temporary wetlands also differed in relation to anuran diversity over the seasons. Overall, this suggests that anuran biodiversity is differently structured in temporary and permanent wetlands, likely through the role of adult movement patterns.

Considering the dependency of wetland hydrology and of the life cycles of many wetland-dependent organisms (e.g., plants and ectothermic animals) on precipitation and temperature regimes (Jackson et al. 2014), climate patterns could be viewed as an additional driver of wetland biodiversity through impacts on hydroperiod and species phenology. So far, most evidence of the potential influence of those regional drivers on biodiversity of wetlands in the *Campos Sulinos* stem from studies in the coastal wetlands of the Pampa. For plants, seasonal variation in precipitation leads to local extinction and/or dormancy of submerged and free-floating species in drier periods of the year (Rolon et al. 2008). Conversely, wetland plant communities in areas with higher seasonality in precipitation are increasingly dominated by amphibious species, more tolerant to longer dry-period lengths (Bertuzzi et al. 2019). Invertebrate composition also shifted according to climate characteristics of the coastal wetlands of the

Pampa grasslands. Specifically, areas with warmer and less seasonal variation in temperature showed higher dissimilarity in spider and insect composition compared to the colder and more seasonal regions (Ávila et al. 2020; Bacca et al. 2021). This is likely because species with phenological and ecophysiological traits more associated with higher temperatures (e.g., spiders with restricted movement patterns and insects with low thermoregulation capacity) were less frequent in the wetlands with colder and less-seasonal temperatures (Pires et al. 2018; Ávila et al. 2020).

In addition, given the "discrete" nature of freshwater wetlands, the spatial positioning and the isolation of wetlands are believed to be strong predictors of their biodiversity (Jeffries et al. 2016). Higher richness of waterbird species was detected in coastal wetland fragments located in landscapes with greater connectivity and matrix permeability than isolated wetlands located in unsuitable landscapes (Guadagnin and Maltchik 2007). Increasing isolation of wetland fragments was also negatively related to macrophyte richness (Rolon et al. 2012) and higher dissimilarity in the composition of aquatic insects in the Pampa grasslands (Bacca et al. 2021; Pires et al. 2018).

The key ecological factors driving the wetland biodiversity across *Campos Sulinos* include the length of hydroperiod (which underlies a series of local environmental modifications and biotic interactions within wetlands), the local climate regimes associated with wetland location, and the degree of isolation of each wetland. Although there seems to be few unique species of temporary and permanent wetlands, variations in wetland hydroperiod seem to drive the local biodiversity of the wetland-dependent wildlife by favoring the predominance (rather than species turnover) of different species along a hydroperiod gradient and, most important, through important changes in the ecological dynamics of single wetlands. In this context, species functional traits related to dispersal mode, tolerance to dry periods, and adaptation to local climate patterns play an important role in determining the number and the identity of the species present at a given moment in each wetland across the *Campos Sulinos*.

13.3 Wetlands and Land Management Practices: Did You Make the Best Choice?

Small freshwater wetlands that dry up for part of the year are often viewed as wastelands and easily overlooked. Given the small surface water area (<1 ha), these freshwater habitats are tightly bound to surrounding terrestrial environments. Historically, grasslands in the *Campos Sulinos* region have been shaped by grazing and fire. Nowadays, these grasslands are facing a rapid transformation to grow food crops and other land uses, with deleterious effects on biodiversity. Research published over the past 5 years makes the warning clear (Staude et al. 2018; Moreira et al. 2021). As grasslands are lost and biodiversity erodes, so will the quality of the wetlands in the *Campos Sulinos* and the associated ecosystem services (biological productivity, water quality maintenance).

Modification of surrounding land for human use, be it agricultural or urban, has an inherent effect on each wetland type (and associated biodiversity). So, it is unsurprising that pristine areas support higher levels of biodiversity than agro-pastoral lands. In Southern Brazil, small wetlands are commonly surrounded by extensive livestock farming, intensive crop-based agriculture (Fig. 13.1c), and afforestation. Reducing the impact of such land uses is a priority, not only for ethical reasons but also to integrate conservation and food production on the same land (i.e., land sharing). Relative benefits and drawbacks of rural land uses to wetland biodiversity largely depend on management practices. However, reconciling biodiversity conservation with economic gains is not straightforward. Synergetic effects of climate change and land use are already drying out many wetlands in Brazil (Project MapBiomas 2021a). But there is an opportunity to manage such issues. Progress can be made by involving strategies of land sharing and land sparing.

Aside from floodplains in the coastal region, wetlands in the *Campos Sulinos* typically exist as small remnants embedded in a larger matrix of farming. Roughly 40% of native grasslands remain in the portion corresponding to the Pampa, and the situation of highland grasslands in the Atlantic Forest is even worse (Project MapBiomas 2021b). Many of the remaining grasslands are used for extensive domestic animal grazing. Steered correctly, this land use promotes wildlife habitat and can preserve native vegetation. However, with sharply increasing prices for commodities (such as soybean, corn, and rice) during the last decade, the remaining grasslands of the Pampa are under substantial pressure for agricultural development. Evidence already shows that the conversion of natural grasslands into short-term crops promotes biodiversity erosion in its different dimensions (i.e., species richness, functional and phylogenetic diversity). Such erosion is consistent across primary producers, terrestrial consumers, and key consumers in wetlands (Staude et al. 2018; Moreira et al. 2020; Saccol et al. 2022). In a closer look at amphibians, phylogenetic relatedness and reproductive modes mediate most responses to land use intensification (Moreira et al. 2021; Saccol et al. 2022). Species that deposit eggs directly in the water, without the protection of foam nests, are the most sensible to grassland modification (Fig. 13.2a). Currently, there is growing consensus that extensive cattle grazing over large native pastures may provide an alternative

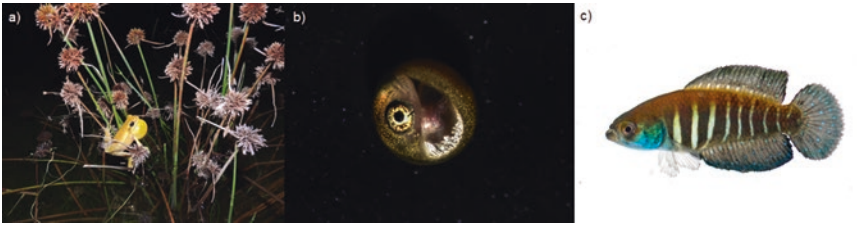

Fig. 13.2 (**a**) Frog species that deposit eggs directly in the water, without protection of froth; nests are susceptible to grassland modification (Photo: Leonardo F.B. Moreira); (**b**) annual fish embryo in dormant stage (Diapause III) (Photo: Vinicius Weber); and (**c**) *Austrolebias gymnoventris*, an annual fish species of temporary wetlands of Pampa grasslands. (Photo: Pedro Hoffman)

more compatible with conservation than short-term crops in wetlands of *Campos Sulinos* (e.g., Fontana et al. 2016; Staude et al. 2018; Moreira et al. 2020). After the conversion of natural ecosystems around wetlands to croplands, alterations of hydrological regimes and vegetation homogenization are the immediate impacts on freshwater communities. As time goes by, the footprint of agrochemicals tends to increase because many wetlands serve as long-term sinks on the landscape. But we should consider that the wet and dry phases of temporary wetlands are closely intertwined. A dry pond bed does not make it biologically dead. Even a dry bed deserves attention and conservation.

It is no secret that the production of desiccation-resistant forms is crucial for community dynamics in freshwater wetlands, especially temporary ones. Many wetlands have diverse propagule banks (e.g., seeds, dormant zooplankton, and killifish eggs) that can be sources for biodiversity recovery once habitat quality improves. As always, uncertainty remains. The contribution of this "storage" effect is dependent on the length of the dry phase, stressors originating on-site or off-site, and the ongoing climate change. Although studies often focus on how organisms respond to agrochemical application during the aquatic phase (Stenert et al. 2018; Azambuja et al. 2021), it is important to acknowledge that intensive land management can also impact wetlands during the dry period. While the studies considering how wetland-dependent wildlife is modulated by land management are in their infancy in Southern Brazil, they already point lower thermal tolerance – and other deleterious effects – in dormant propagules, larval stages, and adults (Babini et al. 2015; Zebral et al. 2018). Going forward, we must remember that the compounding impacts of heat events and droughts are expanding dry periods in temporary wetlands. Landowners and the scientific community should jointly take action to understand which land uses have more pervasive impacts and which uses help to supplement biodiversity and boost revenues.

There is still much to know about the consequences of the transformation of freshwater wetlands to grow food crops, but rice fields are sometimes considered supplementary habitats for many aquatic species in farmland landscapes (Guadagnin et al. 2012; Maltchik et al. 2017). In the absence of any environmental guidance or recognition of the flow of ecosystem services, farmers often jeopardize essential regulating services to increase the supply of provisioning services, such as rice. So, how can we do better? The conversion of wetlands to rice fields in the *Campos Sulinos* region occurred with little consideration of their impacts, yet some management practices provide promising models. Organic farming, wet fallow, and maintenance of original vegetation around field edges are important tools that help to mitigate the impacts of wetland conversion to rice cultivation (Machado and Maltchik 2010; Moreira and Maltchik 2014). Still, strong bottlenecks impair the adoption of more sustainable land management practices, and biodiversity-friendly agriculture has been occupying a gray zone between science and politics. Criteria for loan concessions, tax subsidies, and organic food choice by the public are tricky matters when producers decide to adopt better land management practices (Schiesari et al. 2013). Two additional factors associated with conventional irrigated rice command attention. The soybean crop area in rotation with irrigated rice increased threefold in the last 10 years (as a consequence of drainage practices; IBGE 2021). And the use of early and very early-cycle rice cultivars is increasing rapidly. These tendencies indicate a decrease in soil moisture and mosaics of microhabitats favorable to different wetland-dependent species. If the current scenario holds, not only habitat services (as open water in rice fields is critical, both as spawning and foraging site for many amphibians and fish) but also regulating services like local climate and maintenance of soil fertility would be compromised.

Land mismanagement has transformed many grassland environments, and associated wetlands, into exotic forest plantations. In the last 35 years, all states in southern Brazil have increments (between three to ten times) in the area used for tree monocultures (Project MapBiomas 2021b). Exotic trees of *Acacia*, *Eucalyptus*, and *Pinus* cover now around 5400 km^2 of grasslands only in the Pampa. Further, tree plantations favor the spread of invasive exotic species into the landscape – a dire reality in the coastal plain, even inside protected areas. It is well established that afforestation of open habitats triggers not only landscape changes, principally by shading, but it can also change hydrological cycles through an increase in the evapotranspiration rates (e.g., Jackson et al. 2005). Thus, exotic tree monoculture systems have a huge impact on many wetland species because of their thermal requirements and mobility. Animals like amphibians, reptiles, and aquatic insects require heat exchange from the environment to fulfil several body functions. In addition, they typically have small home ranges and move smaller distances than mammals or birds. Reports of the effects of tree plantations on the wetlands from the *Campos Sulinos* region have increased in the last decade (Stenert et al. 2012; Saccol et al. 2017), and negative outcomes include reduction in specie richness, changes in community structure, and local extinctions in several environments (Stenert et al. 2012; Kellermann et al. 2021). Today, we hear frequent debates about ideas such as the creation of conservation units – not just to protect mega-diverse fauna and flora but to enhance the integrity of watersheds – and indeed, communities and governments are emerging in the Brazilian states with this as a response mitigating to the effects of warming climate. Yet, it is sobering to see how crops and plantation forests occupy large areas inside the few integral protection areas encompassing grasslands and wetlands of southern Brazil (Ribeiro et al. 2021). The challenges ahead are formidable, but the future of wetlands in the *Campos Sulinos* passes through particular landowners and if they are willing to maintain grasslands, i.e., an intact surrounding of wetlands, or not. Of course, land-sparing strategies and formally protected areas are also important tools in ways forward. Every bit of avoided conversion matters.

Although extensive livestock farming seems to be the best choice for land sharing in the *Campos Sulinos*, there is still direct nitrogenous waste input into ecosystems and damage by trampling, besides changes in vegetation structure (Dala-Corte et al. 2016). Thus, grazing regimes and stocking densities are key features in the relationship between livestock and small wetlands. One common challenge for wetland restoration projects is figuring out what effects of land use (isolated or synergetic) they are even working with. Sustainable land management practices are always a work in progress, with answers that are not always definitive. Grazing by cattle and horses has shaped South Brazilian grasslands since the seventeenth century, and thus the *Campos Sulinos* can be seen as a cultural landscape. Cultures change, and today, it's hard to acknowledge that there are two contradictory trends. Many landowners lack any cultural connection to the *Campos Sulinos*, and the values of this landscape, or its traditions. Today, we strive to change the culture of land use to be less intensive and to value the carefully managed cultural landscape. Science has provided a growing body of evidence and practical applications to wetlands and local land management in southern Brazil. Policies that foster enabling conditions are still a long way off, however. In short, one needs to consider that our land use dilemma doesn't have to be a devil's bargain.

13.4 Zoochoric Dispersal Promotes Biological Exchange Between Grassland Wetlands

Dispersal is the process of movement of organisms between habitats in the landscape. It is essential for the colonization of species in new habitats and for the dynamics of metapopulations (Brown and Lomolino 2006). The success of dispersal depends both on intrinsic features of the organism, such as its ability to move, and on landscape structure, such as the distance between favorable habitats and permeability of the matrix (Bowler and Benton 2005). Wetland organisms with high capacity for self-locomotion, such as birds and mammals, tend to have their dispersal facilitated among wetland habitats, even if they are isolated from each other. On the other hand, sessile aquatic species such as plants and some invertebrates depend on passive dispersal to move across the landscape.

Passive dispersal occurs when whole organisms or their diaspores are transported by a vector (Green et al. 2016). When the wind is the dispersal agent, the process is called anemochory, and it is more evident in plant species with seeds adapted to soar in the wind (Soomers et al. 2013). Dispersal by anemochory in wetland systems tends to present a random behavior, since it will depend on the diaspore characteristic, such as size and shape, and on the intensity and direction of the wind. In hydrochory, the water acts as a dispersal agent, and this process is relevant both for whole organisms and for their propagules (Soomers et al. 2013). Zoochory (Fig. 13.3) occurs when the transport vector is an animal. This process is traditionally divided into synzoochory, when for different reasons the vector intentionally transports the dispersed organism; epizoochory (or ectozoochory), when propagules or whole organisms are transported unintentionally attached to the external parts of the vector; and endozoochory, when this dispersal occurs through the animal's digestive tract (Green et al. 2016). Several species of animals act as vectors of passive dispersal in aquatic environments, and although there is indirect evidence for the role of amphibians (Vanschoenwinkel et al. 2008) and mammals (Vanschoenwinkel et al. 2011), waterbirds have special relevance (Green et al. 2016).

Fig. 13.3 Representation of the zoochory process promoted by waterbirds. Typically, a whole organism or its diaspore ends up attached to the outside of the animal or is ingested by the bird, being released and transported from area A to area B

Darwin (1859) regards some considerations about how waterbirds may act as agents of dispersal both by epi- and endozoochory, and from the mid-twentieth century onward, several studies, notably those carried out in the northern hemisphere, launched new perspectives on the role of birds in plant dispersal (Figuerola and Green 2002; Silva et al. 2021a, b). In South America, the first studies related to dispersal by endozoochory in wetlands were on waterbirds and in the Pampa grasslands (Silva et al. 2018, 2019, 2021a, b), demonstrating the importance of zoochory as a dispersal process among wetlands. Silva et al. (2018) found that whole plantlets of the angiosperm *Wolffia columbiana* (Araceae) survived the passage through the digestive tract of birds of white-faced whistling-duck (*Dendrocygna viduata*). This finding broadened the spectrum of how whole plants can be dispersed in wetlands of Pampa grasslands. Silva et al. (2021a) identified 2066 intact diaspores from 40 different plant taxa, including seeds of 37 angiosperms and diaspores of Lycophyta (*Isoetes* cf. *maxima*), Pteridophyta (*Azolla filiculoides*), and Charophyceae in fecal samples of five waterfowl. The authors found that diaspores of native amphibious and emergent aquatic plants were dominant in the fecal samples of waterbirds, but aquatic floating and terrestrial plants were also present.

Endozoochory by waterbirds also is particularly relevant to the dispersal of a wide range of non-flying aquatic invertebrates. Silva et al. (2021b) found 164 invertebrate propagules in fecal samples of waterbirds in the Pampa, including eggs of the Temnocephalida and Notonectidae, statoblasts of bryozoans, and ephippia of Cladocera. The authors identified 12 waterbird species contributing to the dispersal of invertebrates in the Pampa, and these numbers likely will be higher if the number of studied bird samples and bird species were higher. Recently, Barboza et al. (2022)

found that snails are also potentially dispersed by endozoochory by waterbirds in the Pampa grasslands.

Fish dispersal by waterbirds has often been an alternative that explains how some fish species colonized isolated waterbodies (Emmrich et al. 2014). Epizoochory of eggs historically always was cited as a possible mechanism to fish dispersal (Darwin 1859), although no studies provide solid empirical evidence validating such a process (Hirsch et al. 2018). Recently, one study raised the internal transport of eggs as an alternative to fish dispersal in wetland system. Silva et al. (2019) showed that eggs of some killifish species (Rivulidae, Cypriniformes) of the Pampa can pass through avian gut, with a rate of 1% of survival.

In the Pampa grasslands, large populations of teals, rails, storks, herons, ibis, and gulls make seasonal migrations or regional movements that can reach hundreds or thousands of kilometers (Blanco et al. 2020). The factors that regulate these movements are not clear, and although some species have well-defined annual migration periods, most of them probably migrate according to the variations in the regional hydroperiod, wetland availability, and food supply. Such characteristics can make the dispersal in wetlands of the Pampa less directional than that observed in temperate regions (Silva et al. 2021a). Considering the high ability of waterbirds to cover hundreds of kilometers in short periods and their capacity to disperse a wide spectrum of aquatic organisms by zoochory, these studies show the importance of waterbirds in the distribution of wetland species in the Pampa grasslands.

13.5 Annual Killifishes: The Endemic and Endangered Grassland Fish Species

Annual killifishes are small-sized and short-lived organisms that inhabit temporary wetlands in South American subtropical grasslands (Volcan and Lanés 2018). Annual fish developed adaptations to ensure the survival of their eggs in the sediment during dry periods (Furness et al. 2015). One of the most important adaptations is when fish embryos enter the dormant stage (diapause) and adjust their development accordingly to environmental conditions (Godoy et al. 2021) (Fig. 13.2b). Annual life cycles in fish are unique to two families: Nothobranchiidae (Africa) and Rivulidae (Neotropical Region).

Many annual killifish species from the Rivulidae family occur exclusively in temporary wetlands spread in landscapes highly impacted by livestock and agriculture (Lanés et al. 2018; Fig. 13.1a). The low dispersal ability, specialized life cycle, and restricted geographic distribution turn several annual killifish species critically endangered (Volcan and Lanés 2018). Therefore, annual killifishes are target-group and flagship species for conservation of temporary wetlands in South America subtropical grasslands.

In Rio Grande do Sul state, 40 species of Rivulidae can be found (Lanés et al. 2021; Volcan et al. 2021), belonging to three killifish genera: *Austrolebias* (34 species) (Fig. 13.2c), *Cynopoecilus* (5 species), and *Atlantirivulus* (only 1 species, unique with non-annual life cycle). The *Campos Sulinos* region thus is considered the world center for diversity and endemism of annual killifish, mainly of the genera *Austrolebias* and *Cynopoecilus* (Lanés et al. 2018). However, true diversity should be greater, since inventories and studies based on phylogenetic and molecular analyses indicate a high number of potentially new species not yet been described by science (Garcez et al. 2020): the existence of at least a dozen new species of annual killifishes not yet described in RS can be expected.

The annual killifish species found in the *Campos Sulinos* tend to be endemic to this region, although some species are shared with neighboring countries such as Uruguay and Argentina (Lanés et al. 2014). Species distribution is concentrated mainly in the Pampa grasslands, in wetlands belonging to the Laguna Patos-Mirim hydrographic system, and the Uruguay River basin. Among annual killifish species, only three (*Austrolebias botocudo*, *Austrolebias nubium,* and *Austrolebias varzeae*) were found in highland grasslands.

Lanés et al. (2018) conducted the first broad scale study to understand annual fish distribution patterns in the *Campos Sulinos*. They showed that the species assemblage was strongly spatially structured, and many individual species formed discrete units. Furthermore, annual killifish occurrence was negatively associated with altitude at the landscape scale, and negatively associated with water depth and presence of predatory fish at the local scale. The authors also found that assemblage composition is spatially structured, and differed among hydrographic regions, with high influence of altitude, temperature, and monthly precipitation.

13.6 Restoring Biodiversity and Ecological Services in Degraded Wetlands: Now Is the Time

We are at the beginning of the United Nations Decade on Ecosystem Restoration (2021–2030), which is an international appeal to the urgent need to restore natural ecosystems degraded by human activities. In the current and growing scenario of environmental degradation, wetland systems have been widely lost all over the world. Studies estimate a loss of wetland area of around 64% worldwide (Davidson 2014).

Faced with this alarming scenario, many public policies aimed at wetland restoration have emerged in recent decades (Mitsch and Gosselink 2007; Moreno-Mateos et al. 2012). For example, wetland restoration is already an established concept in national and global climate change mitigation strategies (Society for Ecological Restoration 2004) and was listed as one of the relevant topics at international conferences on wetlands. Strassburg et al. (2020) identified global priority areas for ecosystem restoration across all terrestrial biomes, and they estimated their benefits and costs. These authors showed that among the different types of ecosystems (forests, natural grasslands, shrublands, and arid ecosystems), wetland restoration has the highest relative importance for biodiversity conservation. In North America, more than $70 billion has been spent restoring 3 million ha of wetlands over the last decades (Copeland 2010). In China, a total of 1369 km^2 of wetlands were restored from agricultural areas between 1990 and 2010 (Mao et al. 2018).

The earliest wetland restoration activities were focused on restoring a specific ecosystem function. Nowadays, restored wetlands are intended to reestablish a variety of ecological attributes including community structure (species diversity and habitat) and ecosystem processes (energy flow and nutrient cycling), and the broad suite of goods and services to the landscape (Spieles 2022). However, wetland restoration is challenging because it must be guided by an understanding of the main ecological processes that structure the aquatic communities (Spieles 2022). There is a wide variety of different types of wetlands, with distinct characteristics, hydrology, vegetation, and soils, such as floodplains, tidal marshes, peatlands, depressional wetlands, mangroves, forest wetlands (Junk et al. 2014), which makes the restoration of these ecosystems even more challenging. Therefore, the successional trajectories and attributes can be highly variable among wetland restoration projects.

Restoration efforts related to wetlands have been initiated around the world for different purposes such as water quality improvement, biodiversity enhancement, floodwater control, carbon sequestration, and aquifer recharge (Comín et al. 2014; Craft 2016). However, little focus has been given to the recovery of functional processes in wetlands (Cabezas et al. 2009), such as primary production, predator-prey interaction, decomposition, and herbivory (Español et al. 2015). Wetland recovery activities have been achieved using native species and eliminating the causes of degradation (Hughes et al. 2018), but the recovery capacity is greatly affected by abiotic factors such as the size of the restored ecosystems, connectivity to other aquatic systems, and climate (Moreno-Mateos et al. 2012).

A common approach to restoring wetland ecosystems is to introduce species important for restoring ecosystem functions. Some methods used to accelerate the succession and ecosystem development of restored wetlands consist of adding soil nutrient and organic matter and vegetation propagules (seeds, fragments – rhizomes, seedlings) (Craft 2016). Among the methodologies used in wetland restoration, the translocation of sediment containing seed banks and dormant eggs of aquatic invertebrates from a “donor wetland soil” has been shown to be very efficient in the recovery of plant and invertebrate communities in ecosystems degraded by human activities (Richter and Stromberg 2005).

The surface layer of natural wetland sediment (5 cm) can contain 2000–50,000 viable seeds of different aquatic plant species per 1 m^2 (Burke 1997) and 10^3–10^6 eggs per 1 m^2 of zooplanktonic species (Hairston 1996). De Stasio (1990) found between 150,000 and 400,000 resistance eggs of the copepod Calanoida *Diaptomus sanguineus* per 1 m^2 per year. Thus, the seed and egg banks existing in the sediment of natural wetlands constitute a fundamental ecological and evolutionary reserve for the recovery of biological communities in these ecosystems (Brendonck and De Meester 2003; Jenkins and Boulton 2007).

Recently, two initiatives to restore degraded wetlands were carried out in the Pampa grasslands (Vendramin et al. 2021; Silva et al. 2022). In both studies, techniques of topsoil translocation from natural wetlands were used to test the zooplankton recovery in sediments of rice fields and wetlands degraded by mining activities. Both studies analyzed if the increase of topsoil addition from natural wetlands in the sediment of cultivated (rice field) and mined wetlands (clay mining) influenced the hatching of zooplanktonic organisms from their dormant stages. For practical purposes, the results showed that some natural wetlands may not be good donors of topsoil sediment to restore areas subjected to mining activities (Vendramin et al. 2021), that is, the quality of donor wetlands (their topsoil, water, and habitat structure) should be evaluated before to start restoration projects. Sediments from natural wetlands with a more diversified and abundant bank of zooplanktonic dormant stages should be preferred for use in restoration projects.

An important goal of wetland restoration projects developed in the Pampa grasslands was to try to find the optimal amount of sediment needed to be removed from natural wetlands to restore degraded wetlands. This information is extremely important to reduce costs and encourage initiatives by producers in restoration projects. Silva et al. (2022) showed that 30% of topsoil addition from donor natural wetlands can lead to significant changes in the zooplankton composition in areas degraded by rice fields in a short-term experiment. The topsoil addition of 30% in the rice fields made the zooplankton composition resemble the composition of the reference wetlands. These results showed that the transplant technique of zooplankton dormant stages associated with topsoil can be a promising method to be used in the recovery of wetlands in the Pampa grasslands. Due to the effects of wetland habitat quality on the surrounding landscape, restoration of a wetland will also require restoration of adjacent ecosystems. Unfortunately, ecological restoration of grasslands in the *Campos Sulinos* region still is very much at the beginning and still limited in terms of available techniques (e.g., Guerra et al. 2020; Porto et al. 2023). Both more research and more implementation in practice are clearly necessary, also at the interface of terrestrial and wetland ecosystems.

13.7 Importance of Wetland Conservation in the *Campos Sulinos*

The wetlands of the *Campos Sulinos* present high biological diversity for different groups of organisms (invertebrates and vertebrates) and provide many benefits for the human population through ecosystem services (provision, support, regulation, and cultural). The conservation of the wetlands will guarantee the maintenance of a large part of the region's biological and genetic diversity and will provide natural resources to local human population (water to drink and to produce energy and grains, fish, firewood, clay to make tiles and bricks, and many others). In addition, the conservation of wetlands will provide leisure and recreation areas for the urban population, and minimize the negative impacts that floods bring to large- and medium-sized cities.

Studies related to wetland inventory and classification are necessary to support wetland conservation in the *Campos Sulinos*. These studies will provide maps of the exact location of the different types of wetlands present in the region and their conservation status. In addition, studies related to ecological restoration and environmental education will strongly contribute to the conservation of the wetlands of the *Campos Sulinos*.

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Chapter 14
Soil Carbon Stocks in the Brazilian Pampa: An Update

Carlos Gustavo Tornquist, Cristhian Hernandez Gamboa, Daiane Deckmann Andriollo, José Miguel Reichert, and Fioravante Jaeckel dos Santos

14.1 Introduction

The northeastern part of the Río de la Plata grasslands (Paruelo and Jobbágy 2007) extends into Brazil (Fig. 14.1), comprising approximately 18% of this ecoregion. This region is widely known for livestock production on natural grasslands, introduced by European settlers more than 300 years ago, a land use broadly compatible with continuous ecosystem services provisioning and economic returns to ranchers. However, dramatic changes in land use have disrupted these extensive livestock-based production systems, posing the risk of soil and water degradation (Foucher et al. 2023).

Globally, grasslands store about 1/3 of the total terrestrial C stocks in the soil (Bai and Cotrufo 2022). Environmental drivers such as temperature and

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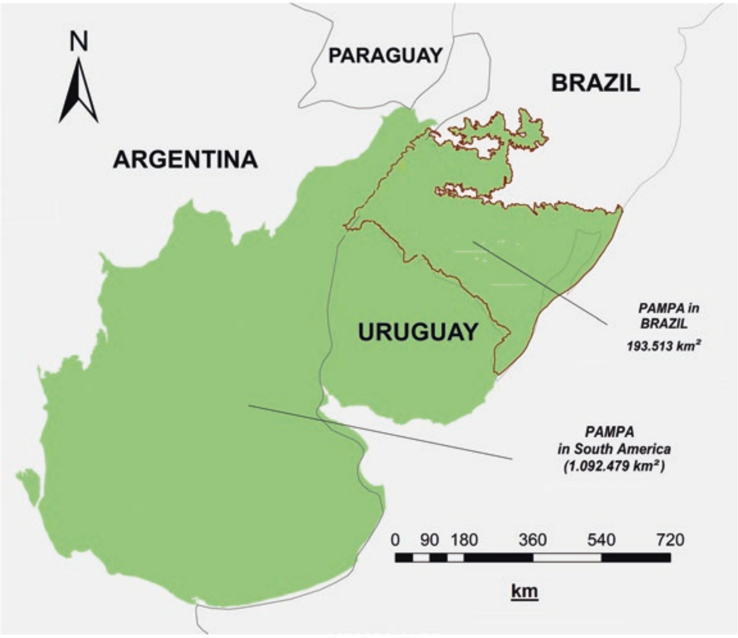

Fig. 14.1 Extension of the Río de la Plata grasslands in Southeastern South America and in Southern Brazil. (Pampa of Rio Grande do Sul state)

precipitation favor the accumulation of large soil C stocks in the Pampa (Tornquist et al. 2009; Pillar et al. 2012). These stocks are impacted by changes in land use that have been occurring in Southeastern South America in recent times, notably the conversion to crops and silviculture (Coutinho et al. 2015; Azevedo et al. 2023). Conversion practices and the intensity and frequency of soil cultivation following conversion can enhance soil organic carbon (SOC) decomposition and turnover, leading to reductions in soil C stocks and increasing greenhouse gas emissions, especially CO_2. On the other hand, it has been shown that sustainable rangeland management through optimized stocking rates and supplemental feedstuffs could support higher biomass and animal production while conserving biodiversity, sequestering additional soil C, with overall benefit to the resilience of these ecosystems. Additionally, these sustainable management practices contribute to the adaptation of livestock production systems in the context of a changing climate (Schuman et al. 2002; Soussana 2009; Conant and Cerri 2017).

14.2 Regional Context

The Río de la Plata grasslands ecoregion encompasses the southern and western regions of Brazil's southernmost state, Rio Grande do Sul (IBGE 2023) (Fig. 14.1). In Brazil, this region is usually referred to as the 'Pampa biome' or only 'Pampa'.

Land use conversion has led to massive ecosystem fragmentation, accompanied by the invasion of exotic species, of which the African grass *Eragrostis plana* is a prominent example (Medeiros et al. 2009). Most of the remaining grasslands that still retain high biodiversity and the natural structure and composition are on private lands, with management varying from traditional extensive grazing to more intensive practices such as fertilization, liming, mowing and overseeding exotic grasses and legumes (Cordeiro and Hasenack 2009; Hasenack et al. 2023).

It has been widely reported that conservation of these southern Brazilian grasslands has been neglected, with very few protected areas (Freitas et al. 2018; Ribeiro et al. 2021; Overbeck and Vélez-Martin 2015, 2022; Ellwanger et al. 2022). Increased rates of land use conversion (to agricultural and silvicultural land uses) in the last five decades reduced the natural grassland vegetation in the state of Rio Grande do Sul (the focus of this contribution) to approximately 32% of the original land cover remaining in 2021 (Azevedo et al. 2023; Fig. 14.2).

The soils in this region are predominantly Argissolos (Ultissols – 26%), Neossolos (Entisols – 20%) and Latossolos (Oxisols – 15%), according to the most recent soil map of Rio Grande do Sul (IBGE 2018). These soils and the geomorphological context of the Pampa are discussed at length in Almeida (2023) and Hasenack et al. 2023 (Chap. 6, this volume). In general, these soils have highly variable natural fertility and are often shallow or poorly drained and therefore do not qualify as prime agricultural soils. Nonetheless, the advent of no-till soil management has

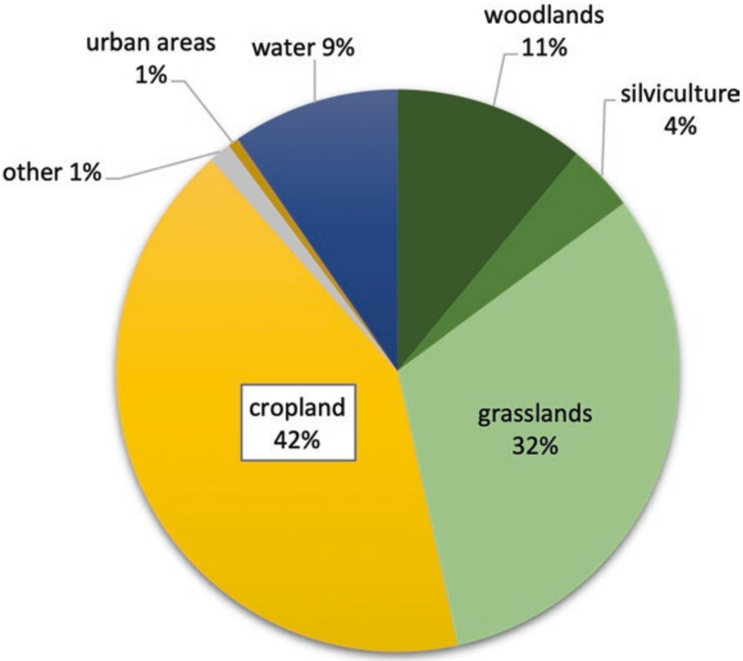

Fig. 14.2 Land uses in the Pampa in 2021. (Azevedo et al. 2023)

favored the expansion of grain crops, especially soybeans, onto the Pampa landscape. Moreover, Vertisolos (Vertisols) and Planossolos (Aquults/Aqualfs) that occur in the lowlands, especially in poorly drained areas, have been extensively cultivated with paddy rice since the 1960s. Some of these lowland soils are clayey or very clayey, with expansive 2:1 clay minerals that make these soils hard, poorly drained and prone to compaction.

14.3 Data Processing in Geographic Information Systems

We applied basic geoprocessing operations to revise and update previous SOC stocks estimates for the state of Rio Grande do Sul (Tornquist et al. 2009) and the Brazilian Pampa (Pillar et al. 2012) using SOC stocks data from recent soil sampling campaigns, extensive literature review and the latest version of the soil map (IBGE 2018). This state-wide map is freely distributed in vector format, comprising 1811 polygons that represent soil mapping units. The nominal cartographic scale of the map is 1:250,000 (IBGE 2018). However, it is noteworthy that the number of soil pedons sampled would be compatible only to a 1:1,000,000 soil survey, so the actual scale is smaller, as discussed by Sarmento et al. (2014). Soil organic C stocks were assigned to the attribute table of the soil vector map. Other polygons representing geographic features such as water bodies, urban areas and sand dunes were assigned zero SOC stock. The geospatial data processing in this study used ArcGIS (ESRI 2011).

14.4 Estimates of Original Soil Carbon Stocks

The original soil C stocks, existing prior to anthropic land use conversion, have also been called ‘no land use’ (NoLU) stocks (Sanderman and Hengl 2017) or Projected Natural Vegetation Soil Carbon (PNVSC) as proposed by Waring et al. (2014). Accurate estimates of the pre-conversion C storage in soils at a regional scale could provide key quantitative data (including variability and distribution mapping). These studies often rely on legacy data from early soil surveys and could be enhanced by new data from targeted soil sampling in areas of relicts of the native vegetation – the space-for-time substitution approach (Dávila et al. 2019).

A previous study (Pillar et al. 2012) produced an estimate of Pampa soil C stocks under NoLU (Fig. 14.3a), at 0–30 cm depth, one of the target depths for reporting greenhouse gas inventories recommended by the IPCC (2019), using a slightly different delimitation for the Pampa region. The SOC data were derived exclusively from a state-wide soil C stock inventory that included pedons sampled from the mid-1960s to the 1980s in Rio Grande do Sul (Tornquist et al. 2009), most of which originated from the RADAMBRASIL Project report for RS state (IBGE 1986). The calculated soil C stock to 30 cm soil depth in the Pampa was 1075 Tg, with a mean

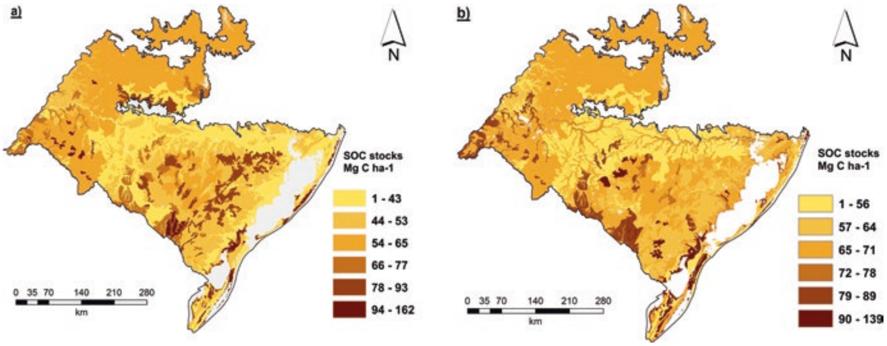

Fig. 14.3 Estimates of original SOC stocks (before land use conversion) in the South Brazilian Pampa. (**a**) Adapted from Tornquist et al. (2009) and Pillar et al. (2012); (**b**) Revised and updated with SOC stocks of the Pampa

Table 14.1 Updated soil classes in the soil map and attributed SOC stocks (under NoLU)

Soil class (SiBCS)	(Soil taxonomy)	SOC stock (kg m^{-2})
Argissolo Amarelo	Ultisol	8.4
Argissolo Vermelho	Ultisol	4.9
Argissolo Vermelho-Amarelo	Ultisol	6.3
Cambissolo Háplico	Inceptisol	5.0
Chernossolo Argilúvico	Mollisol	11.1
Chernossolo Ebânico	Mollisol	8.9
Gleissolo Háplico	Aquepts/Aquults	5.1
Gleissolo Melánico	Aquepts/Aquults	12.9
Latossolo Vermelho	Oxisol	6.9
Luvissolo Crômico	Alfisol	7.6
Luvissolo Háplico	Alfisol	5.4
Neossolo Litólico	Lithic Entisol	6.7
Neossolo Quartzarênico	Quartzipsamment	5.1
Nitossolo Vermelho	Kandic Oxisol	7.1
Planossolo Háplico	Aqults	6.9
Plintossolo Argilúvico	Plynthic Ultisol	6.4
Vertissolo Ebânico	Vertisols	8.4
Mean		*6.6*

soil C density of 6.8 kg C m^{-2}. Most of the soil C was stored in Neossolos (Entisols), Argissolos (Ultisols), Planossolos (Alfisols) and Latossolos (Oxisols) (Table 14.1). The research relied on a limited number of legacy pedons, originally obtained without due emphasis on soil C – the analyses were conducted by the routine Walkley-Black method, and soil bulk density data were not provided. The later omissions were resolved by applying pedotransfer functions developed for Brazil (Benites et al. 2007). Nevertheless, the soil C stock database developed at that time was essentially the most comprehensive available for the state of Rio Grande do Sul for soils in their original native condition.

To revise the previous estimate, we used a novel SOC dataset that was developed within the GrassSyn project[1] in 2022 (unpublished data, Botany Dept., UFRGS). This dataset was the result of a systematic literature review that covered WoS, Scopus, Scielo and Lume databases, which provided 131 SOC stock samples that were collected in soils of the Brazilian Pampa following established protocols for soil C stock (IPCC 2019; FAO 2019). A synthesis of the SOC data by soil class is presented (Table 14.1). The mean SOC stock was 3% smaller than 6.8 kg C km^2 reported by the previous review (Pillar et al. 2012). These stocks were attributed to the soil mapping units of the digital soil map to estimate (Fig. 14.3) NoLU total SOC at 1.155,1 Tg C.

14.5 Current SOC Stocks

To further advance our understanding of the effects of the land-use changes that occurred in the Pampa on SOC stocks, we used the most up-to-date land use/land cover map developed by the MapBiomas project (Fig. 14.4. MapBiomas v7, Azevedo et al. 2023), combined with SOC stocks data obtained from cropland and silvicultural land obtained in the above-mentioned GrassSyn project and, more importantly, the literature review to produce a current SOC stock map and related soil C estimation (Fig. 14.5)

These datasets did not reflect the great diversity of soil classes in the region, so SOC data from crop- and silvicultural land was incomplete. To fill the gaps of missing SOC data and produce a continuous soil C map of the Brazilian Pampa, we assigned the same SOC stocks of similar soil classes. Therefore, the map produced (Fig. 14.4) should be considered provisional. More accurate and reliable estimates could be obtained from a systematic soil sampling campaign targeting soil C that is the scope of the ongoing PronaSolos surveys (Polidoro et al. 2021).

It is important to mention that most of the soil C, considering the 0-30 cm depth focused on this study, is in the Neossolos Litólicos (Entissols), Latossolos Vermelhos (Oxisols) and Planossolos Háplicos (Aquualts/Aqualfs) (Fig. 14.6). Neossolos are, by definition, very shallow (surface horizon <15 cm) and generally support plant communities adapted to adverse conditions. SOC assessments in deeper soil layers would likely reveal much less C. Planossolos occur in lowlands, humid environments that favor SOC accumulation. Latossolos are deep, well-drained soils that, under natural conditions, can support dense vegetation. Most Latossolos have a high clay content, which favors soil C stabilization.

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[1] Project 'GrassSyn- Biodiversity of Brazilian grasslands and savannas: patterns and drivers, ecosystem services, and strategies for conservation and restoration', conducted within the Brazilian Synthesis Center on Biodiversity and Ecosystem Services (Fev. 2020–Aug. 2023).

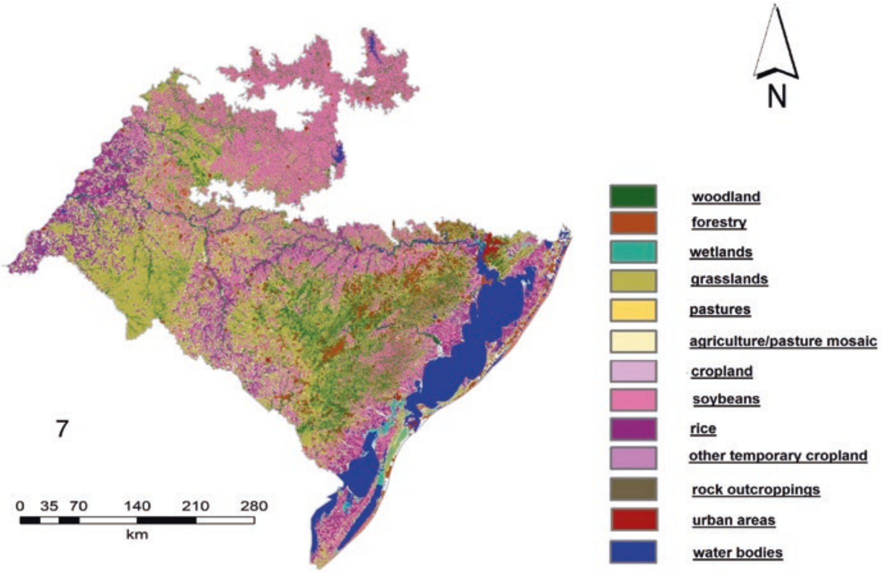

Fig. 14.4 Land use in the Brazilian Pampa in 2021, according to the MapBiomas project. (Azevedo et al. 2023)

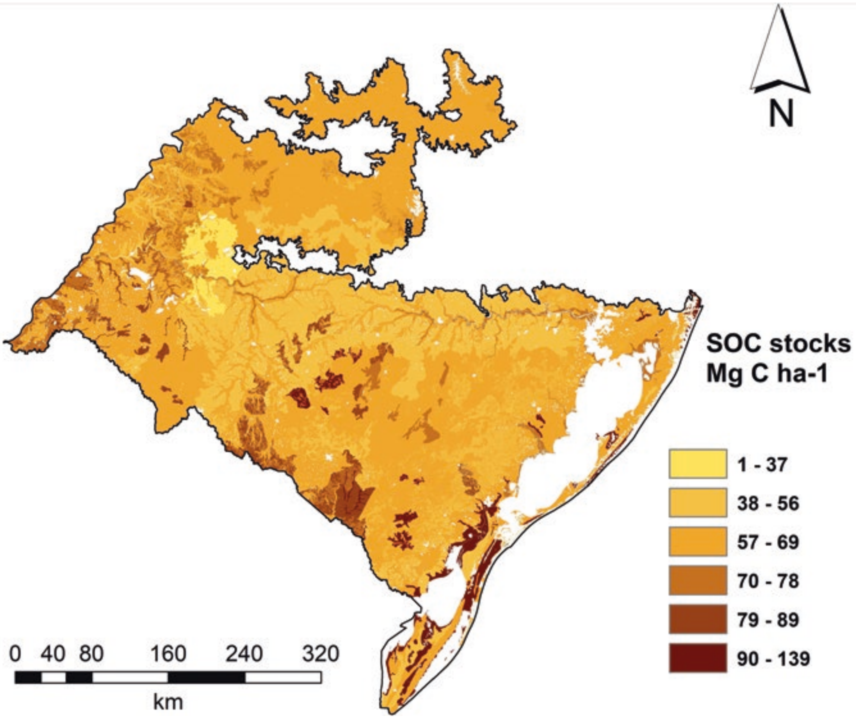

Fig. 14.5 Revised and updated SOC map of the Pampa, with land use in 2021. (MapBiomas 2023)

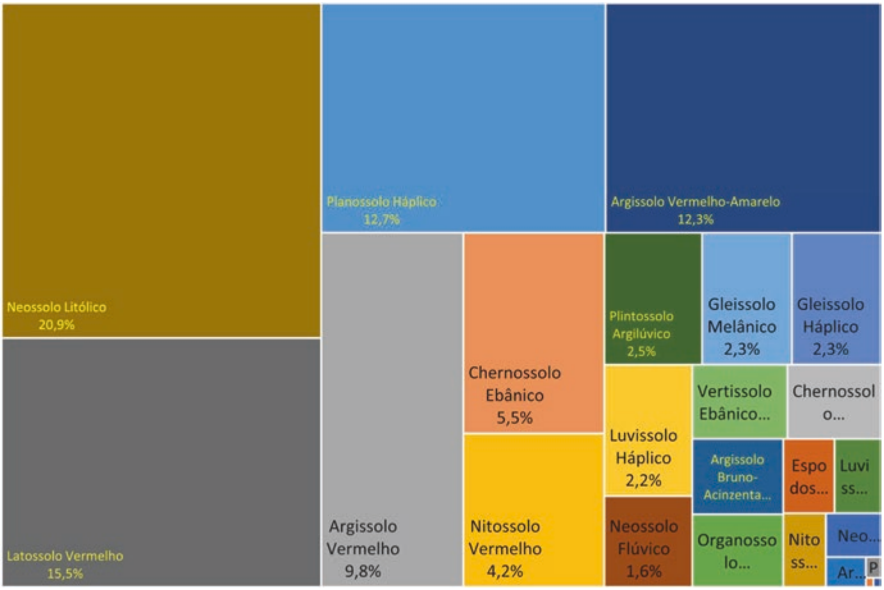

Fig. 14.6 Relative distribution of SOC stocks across soil classes occurring in the Brazilian Pampa. The smaller boxes with no labels represent Espodosolos Ferrilúvico, Luvissolos Crômicos, Nitossolos Brunos, Neossolos Quartzarênicos, Neossolos and Cambissolos Fúlvicos, which account for less than 15% of the total biome SOC stocks

Table 14.2 Estimates of total SOC stocks in the Pampa

SOC stocks in the Pampa				
NoLU (original)				Current stocks
Bernoux et al. (2002)	Pillar et al.[a] (2012)	Gomes et al. (2019)	*This study*	*This study*
------------------------------------ Tg C ------------------------------------				
954	1248	846	1161	1115

[a] Adjusted for current Pampa boundaries

14.6 Synthesis and Uncertainties

SOC stocks obtained in this study were compared with previous estimates of NoLU SOC stocks (Table 14.2). Our estimate was approximately 8% lower than our previous study (Pillar et al. 2012) adjusted for the current Pampa boundaries, whereas it was 7 to 27% higher than estimates extracted from whole-country studies (Bernoux et al. 2002; Gomes et al. 2019). Notwithstanding the small dataset that could be obtained, we assume this review better reflects the SOC stocks in the Pampa because it comprises mostly data from surveys specifically designed to estimate SOC stocks, whereas other SOC stocks studies used legacy data exclusively from the EMBRAPA soil database (EMBRAPA 2023), with estimated soil bulk densities and in many cases, extrapolated depth ranges, to conform to one of the IPCC standard sampling (and reporting) depths (0–30 cm).

We calculated C stocks for year 2021 using space-time substitution approach (Yang et al. 2022), in which current samples from soils under extant native vegetation were used as proxies of soils before conversion, now managed as cropland. This approach revealed a reduction of 3.5% in relation to original C stocks (1161 Tg C). This small difference is somewhat surprising, because conversion from native grasslands to cropland in general leads to a decrease in SOC. However, in the case of the Brazilian Pampa, agricultural practices implemented were based on no-till soil management, which notoriously mitigates SOC losses because organic matter decomposition rates are not markedly enhanced. Care must be taken with these casual comparisons, especially to avoid making a rash assertion that the Brazilian Pampa 'lost' 3.5% of its original soil C: this difference is likely within the uncertainty associated with our C stock estimates. Inferences about the effect of different soil management and land use covers could be more accurately established with paired-plot studies.

A key factor contributing to uncertainties in these SOC stock estimates was the large spatial variability of SOC stocks within the soil classes and their complex spatial distribution. Soil depth is highly variable in this state (Bonfatti et al. 2016). Moreover, mapping units in small-scale soil maps such as the base map from IBGE used (1:250,000) are associations and include taxonomic units that were merged with the predominant soil class to derive the SOC stock maps. Mapping pure taxonomic units would require more detailed (larger scale) soil surveys.

Refinements of these estimates of original C stocks (prior to conversion to other uses) would require intensive soil sampling in areas deemed to be representative of native vegetation before land cover was affected by human activities. Concurrently, an improved contemporary C stock estimate would demand new sampling campaigns in cropped or other managed lands. Both are necessary for an accurate representation of the status of this biome in the national greenhouse gas inventories.

Soil organic C studies in the Brazilian Pampa are recent and unevenly distributed across the ecoregion. Nevertheless, the dataset and map produced in this study indicate that the region holds substantial SOC stocks whose conservation is relevant to avoid additional land use and land cover (LULC) change contributions to climate change. Moreover, there is potential for improved grazing management to facilitate additional soil C sequestration (Pillar et al. 2012; Conant and Cerri 2017). And the ensuing discussion on grassland restoration offers additional opportunities for climate change mitigation (Andrade and Koch 2006). These are crucial research topics arising from the Brazilian commitment to pursue more sustainable agriculture systems to mitigate human-induced changes in the terrestrial C cycle.Data AvailabilityTornquist, Carlos G. (2023), "Soil Carbon Stocks in the Brazilian Pampa: An update", Mendeley Data, V1, doi: 10.17632/kfhdbd3k6c.1.

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Part IV
Vegetation Dynamics at the Forest-Grassland Interface

Chapter 15
Forests in the South Brazilian Grassland Region

Rodrigo Scarton Bergamin, Martin Molz, Milena Fermina Rosenfield, Joice Klipel, Larissa Donida Biasotto, and João André Jarenkow

15.1 Introduction

Forests and grasslands are the two main physiognomies that spread over vast and continuous areas in southern Brazil, which are dominated by vegetation types associated with the Atlantic Forest and Pampa regions ("biomes" sensu IBGE 2019). In the states of Paraná (PR), Santa Catarina (SC), and the north of Rio Grande do Sul (RS), at higher elevations of the South Brazilian Plateau (700–1800 m a.s.l.), grasslands are an important feature in the landscape (Overbeck et al. 2015a). They are found in mosaics with the typical forest formation in the region, the *Araucaria* forest, which is part of the landscape in riparian or insular patches, in variable extensions (Rambo 1956; Klein 1960; Duarte et al. 2006). As elevation decreases, grasslands and the *Araucaria* forest are gradually replaced by species of the Seasonal

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forest formation, with a marked visual impact by the disappearance of the physiognomically dominant forest species, *Araucaria angustifolia* (Rambo 1956; Klein 1960). To the eastern border of the plateau, a narrow strip of low trees characterized as cloud forest and the richer Atlantic coastal moist forest (Mata Atlântica s.s.) are in contact with the grasslands (Falkenberg and Voltolini 1995). To the west and south of the plateau, Seasonal forest borders the grasslands and the *Araucaria* forest. In transition areas between forest types, old-growth individuals of *A. angustifolia* are found together with typical Seasonal forest species but still with a rarefied composition in relation to the forests along the Paraná and Uruguay river basins due to the effect of elevation (Rambo 1956; Klein 1960). These forest formations are the most characteristic expression of the Atlantic Forest domain in Southern Brazil and predominate up to 30° southern latitude (Leite 2002).

Below 30°S latitude, the landscape becomes dominated by grasslands again: we are entering the Pampa, the northern part of a vast grassland region that spreads over Uruguay and Argentina and usually is called “Río de la Plata grasslands” (Andrade et al. 2018). However, forests are also part of the Pampa region, varying in species composition and structure, with a lower diversity than the northern forests and occurring within the grassland matrix (Leite 2002; Vargas et al. 2022). The Brazilian Pampa comprises a heterogeneous region, including different geomorphologic provinces: roughly, the coastal plain in the east (Quaternary deposits), the *Serra do Sudeste* in the center (granite and gneiss rocks), and the *Planalto da Campanha* to the west (basaltic rocks) (Justus et al. 1986). In the coastal plain, grasslands occur over sandy dry, wet, and flooded soils, with swamps, palm groves, and *Restinga* forests scattered among the great coastal lagoons (Menezes et al. 2015). These forests are insular (groves), in sandy or peat (flooded) soils, with a low floristic richness that decreases with the increase in latitude (Waechter 1990). The western boundaries of the coastal plain give way to the granite slopes of the *Serra do Sudeste*, in which a tall and species-rich Seasonal forest develops, considered an extension of the Atlantic Forest (Leite 2002; Vargas and Brack 2021). Further inland, forest patches occur in a mosaic with grasslands, in the *Serra do Sudeste* sometimes dominated by *A. angustifolia* or *Podocarpus lambertii*, or by Seasonal forest species. These patches expand themselves in valleys as riparian corridors towards to the west, reaching the borders with Uruguay and Argentina (Rambo 1956; Giongo and Waechter 2007; Carlucci et al. 2011). The same occurs with Seasonal forests in the basins of the Jacuí-Ibicuí rivers, which extend southward as riparian forests (Leite 2002; Vargas et al. 2022).

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The presence of isolated trees in a grassland matrix, as parkland, is a peculiar aspect of some regions in the Pampa. Palm groves with *Butia* (Arecaceae) species form one typical landscape. *Butia odorata* forms the largest and most extensive palm groves in the coastal plain and the *Serra do Sudeste* and also is present in adjacent Uruguayan and Argentinean territories. Smaller palm groves with *B. exilata*, *B. lallemantii*, *B. paraguayensis*, *B. witeckii,* and *B. yatay* occur in the inner Pampa, mainly in the *Planalto da Campanha* (Waechter 1990; Soares et al. 2014). As part of the Argentinean Province del Espinal, in the extreme west of the *Campanha* region, we find the "espinilho" parklands. Here, the Fabaceae trees *Neltuma affinis*, *N. nigra*, *Parkinsonia aculeata*, and *Vachellia caven*, scattered over a grassland matrix, are conspicuous elements of the landscape (Cabrera and Willink 1973; Leite 2002).

Forests and grasslands historically coexist side by side in the South Brazilian landscapes, expanding and contracting in accordance with climate change (Behling 2002, Behling et al. 2007, Jeske-Pieruschka et al. 2010). Forests were mostly restricted to wetter and protected refugia (Carnaval and Moritz 2008; Wilson et al. 2021). As humidity and temperature increased, woody vegetation gradually expanded along the river valleys, covering slopes and finally in the late Holocene conquering large areas, mainly on the South Brazilian Plateau. In the Pampa, the expansion of forests took place later (Mourelle et al. 2017), and they currently predominate only in the east of Rio Grande do Sul state. In the west, they appear as riparian forests in extensive areas of grassland (Vargas et al. 2022).

In the South Brazilian grassland region, the current climate is subtropical with well-distributed rainfall throughout the year. According to the Köppen system, the Cfa climate type predominates in the Pampa and the Cfb in the plateau (Alvares et al. 2013; Andrade et al. 2019). The persistence of grasslands is often associated with human activities, such as cattle raising and the use of fire (Fidelis et al. 2010, see also Andrade et al. 2023, Chap. 8, this volume). The forests, in turn, tend to continuously advance over the grasslands from the edges of forest patches or by tree species nucleation, mainly from the *Araucaria* forest and the Seasonal forest (Rambo 1956, Klein 1960, Duarte et al. 2006, Bergamin et al. 2019, see also Müller et al. 2023, Chap. 16, this volume). Generalist species associated with these regionally dominant forest formations act as precursors in successional processes and may expand from insular and riparian forests (Orihuela et al. 2015). Considering the large areas covered by forest-grassland mosaics, the floristic composition and forest structure in the contact areas vary according to the forest type and the prevailing environmental factors.

In the next section, we characterize the main tree taxa and forest types in the region in terms of biogeographical history, floristic patterns, and composition, as well as the influence of forest elements in nearby grasslands. Then, in Sect. 15.3, we detail the drivers of tree species richness and species composition of forest communities occurring in the *Campos Sulinos* grassland landscapes. In Sect. 15.4, we focus on an ecosystem perspective, describing patterns of forest ecosystem functioning and the provision of ecosystem services from these subtropical forests. Finally, in Sect. 15.5, we map the overall changes in forest cover in the South

Brazilian grassland region in relation to its potential natural cover and anthropogenic reduction due to land conversion.

15.2 Forest Communities and Trees in the South Brazilian Grassland Region

In southern Brazil, forests of the Atlantic Forest domain are represented by three main formations: Atlantic coastal moist forest, *Araucaria* forest, and Seasonal forest, which roughly correspond to the Atlantic, Parana Forest, and Araucaria Forest provinces described by Morrone et al. (2022). Eastern coastal areas, corresponding to the Atlantic coastal moist forest, harbor subtropical moist forests composed mainly by Atlantic and eastern Amazonian tropical elements; inland subtropical seasonal forests, coinciding with the Seasonal forest, are also composed mainly by tropical elements, but with Andean, Chacoan, western Amazonian affinities and also some Atlantic elements; and warm-temperate/subtropical mixed forests, corresponding to the *Araucaria* forest, covering mainly a large area of the interior highlands, comprise Andean and Austral-Antarctic temperate elements, as well as others of the nearest formations. Other forest types with a lesser range include cloud forests (on the eastern edge of the South Brazilian Plateau), riparian forests, *restingas* (vegetation under marine influence), mangroves in SC and PR, swamp forests. Yet, a small area of Espinal (“*Espinilho”*) in RS and *Cerrado* in PR forms savanna-like vegetation where trees are scattered over a grassland matrix.

15.2.1 Biogeographic History and Affinities of South Brazilian Forests

The affinities of the South American flora unveil a primary origin in the ancient paleocontinent of Gondwana (e.g., Amorim et al. 2009; Morrone 2015; Carta et al. 2022), with two main ancestral biotas having a distinct history associated with the northern and southern portions of the continent. Forests in southern Brazil have affinities with elements from both the north (Atlantic, Amazonian, and Chacoan) and the south (Andean and Austral-Antarctic), as well as with Laurasian families originating in the northern hemisphere that migrated southward (Raven and Axelrod 1974).

Northern South America has an assemblage consisting mainly of Neotropical elements, while southern South America (here defined as the region within 18°–55°S lat., following Segovia et al. 2013) has an assemblage of lineages mostly with southern temperate affinities, which have been suggested to have evolved during and after the breakup of Gondwana (e.g., Romero 1986; Crisci et al. 1991; Villagrán and Hinojosa 1997). From a paleo-perspective, the Neotropical region (Holotropical realm, Morrone 2014, 2015) corresponds to the eastern portion (Crisci et al. 1993) or tropical Gondwana (Amorim et al. 2009), while the Antarctic and Andean regions (Austral realm, Morrone 2014, 2015) correspond to the western portion (Crisci et al. 1993) or temperate Gondwana (Amorim et al. 2009). The southern region of Brazil, located at the mid-latitudes of the continent, has a mixed assemblage of lineages evolved from both tropical and temperate elements.

Through the Cenozoic era, South American vegetation has gone through many expansions and retractions of tropical/subtropical and temperate forests. In the Late Paleocene and Early Eocene, climate was generally warmer and wetter than today, and South America was probably covered by tropical/subtropical continuous humid forests (Morley 2000; Zachos et al. 2001). During the late Paleocene and Eocene, a continuous belt of subtropical humid forest covered northern South America, extending up to 40°S at its widest range (Hinojosa and Villagrán 1997; Ortiz-Jaureguizar and Cladera 2006). Here, it mixed with temperate elements of the southern parts of the continent (Palazzesi and Barreda 2007), giving rise to diverse communities of mixed forests with or without the presence of Neotropical elements in subtropical and temperate latitudes (Romero 1986, 1993, Villagrán and Hinojosa 1997; Wilf et al. 2005).

During the Oligocene, the tropical/subtropical vegetation that covered much of South America at the end of the Late Cretaceous was replaced by vegetation largely of Austral-Antartic origin (Romero 1986; Hinojosa and Villagrán 1997). Under favorable climatic conditions, forests were connected along the subtropics of South America (e.g., Landrum 1981a, b, 1988; Romero 1986; Hinojosa and Villagrán 1997), reaching the southern limit of the tropical forests during the warm periods of the Paleogene (Jaramillo and Cárdenas 2013). With the rise of the Andes, the formation of a belt of arid vegetation caused by the onset of the Andean rain-shadow and a marine transgression in the early–middle Miocene (e.g., Chacón et al. 2012; Murillo-A et al. 2016), the southernmost terrestrial environments of the continent were disconnected from those above Western Uruguay, Southern Brazil, Southern Paraguay, and Southeastern Bolivia northward (Ortiz-Jaureguizar and Cladera 2006).

As a consequence of the Andean uplift and more intensive droughts, subtropical mixed forests became largely extinct in lowland areas (Segovia and Armesto 2015), resulting in the dry landscapes present today in South America. These dry landscapes are fundamental in the shaping of distribution patterns (Ab'Sáber 1977), acting as both dispersal barriers and corridors (Luebert 2021). The Amazon and the Atlantic forests, including the ones of southern Brazil, are currently separated by the South America dry diagonal (SADD), comprised by the Caatinga, Cerrado, and Chaco domains (e.g., Bucher 1982, Prado and Gibbs 1993, Werneck 2011, Zanella 2011, Sobral-Souza et al. 2015), which represents a substantial barrier for biotic exchange between both moist forests (e.g., Oliveira-Filho and Ratter 1995; Raven and Axelrod 1974). However, studies suggest the existence of past biogeographical connections between these forest domains during the Last Glacial Maximum (LGM) (e.g., Sobral-Souza et al. 2015; Ledo and Colli 2017). Seasonal forests of southeastern and southern Brazil were also connected many times in the past to the southwestern Amazon (e.g., Bigarella et al. 1975; Por 1992; Batalha-Filho et al. 2013) and the forests of the Central-Southern Andean moist forests (Southern Yungas of Northwest Argentina and Southern Bolivia, the Tucuman-Bolivian moist forests) (e.g., Nores 1992, 2020; Werneck et al. 2011; Acosta and Vergara 2013; Vergara et al. 2017). These periods of connectivity allowed not only the interchange between these forest formations but also resulted in an increase of diversity in these domains (Nores 2020) for several groups of organisms. Past connections between the southern region of the Atlantic Forest and Southern Yungas are also supported by phylogenetic data and probably contributed to the diversification of lineages in the Atlantic Forest (Costa and Leite 2013; Batalha-Filho et al. 2013; Bacon et al. 2018; Trujillo-Arias et al. 2018).

15.2.2 Diversity and Distribution

The three southern states of Brazil have 1144 native tree-species, distributed in 402 genera and 114 families. The richest plant families regarding tree species are Myrtaceae (216 species), Fabaceae (130), Lauraceae (70), Euphorbiaceae (38), and Rubiaceae (38) (Brazilian Flora 2020). The bulk of richness is in the Atlantic coastal moist forests, where 96% of the families, 87% of the genera, and 76% of tree species are found. Moist forests of the Brazilian Atlantic coast are among the zones with the highest number of vascular plants per area (species richness) across the American continents (Mutke and Bathlott 2005). Seasonal forests also have a high richness of families (88% overall) and genera (77%) but are poorer in tree species (48%). *Cerrado latu* sensu and *restingas* are both rich in terms of plant families (>80%), but together with *Araucaria* forests have less genera and species (considering only trees). Other formations are taxonomically less representative in terms of tree species richness, but some families or genera may stand out, like the South American *Schinus* (Anacardiaceae) in the Pampean domain.

Woody legumes (Fabaceae) dominate most Neotropical forest biomes (Azevedo et al. 2020), and they also have the greatest diversity and number of tree species (de Lima et al. 2015), followed by Myrtaceae (Sobral et al. 2015). Both families account for about one-third of the tree species in the South Brazilian forests and are representative of the diverse origins of its flora: Fabaceae has its origin in the Holotropical realm (e.g., Doyle and Luckow 2003; Schrire et al. 2005a, b; Lewis et al. 2005), and Myrtaceae in the Austral realm (e.g., Ladiges et al. 2003; Lucas et al. 2007; Thornhill et al. 2015). The tropical origin of leguminous trees denotes its richness in Brazil (predominantly tropical), exceeding Myrtaceae by more than eight times in the number of genera and by about 40% in the number of tree species. Most woody legume genera are megathermal; consequently, several genera—like *Bowdichia, Cenostigma, Cyclolobium, Exostyles, Hymenaea, Leptolobium, Luetzelburgia, Myroxylon, Stryphnodendron, Swartzia, Sweetia, Vatairea,* and *Zygia*—reach their range limit on the boundary between the tropics and subtropics (in PR state). Less than half of the leguminous tree genera native to Brazil occur in the southern region, where the richest are *Inga, Machaerium,* and *Mimosa* (represented mainly by shrubs).

An opposite pattern is found for Myrtaceae, with most tree genera native to Brazil occurring in the subtropical and warm-temperate forests of the southern region. There, Myrtaceae is 60% richer in a number of tree species than Fabaceae. As richness may reflect the number of species within a family that are adapted to a given climatic regime (Wiens and Graham 2005), the higher number of species of Myrtaceae may indicate its phylogenetically conserved niche due to evolutionary adaptations to colder and/or wetter environments that shaped the flora of southern South America. Although the family has dispersed and diversified far into varied tropical formations (*Cerrado*, *Caatinga*, tropical moist forests, tropical dry forests, etc.), most Myrtaceae species preserve ecological traits of South American basal lineages of the tribe Myrteae that still basically inhabit moist/wet environments, revealing a strong phylogenetic niche conservatism. The richest genera are *Eugenia, Myrceugenia,* and *Myrcia*, which outnumber in species richness any leguminous tree-genus in southern Brazil.

Comparing the number of genera and species of Fabaceae and Myrtaceae along the latitudinal gradient of the Atlantic Forest (Fig. 15.1) may help to understand the evolutionary differences and ecological adaptations of the mixed assemblage of tropical and warm-temperate elements in the southern region. As one moves to higher latitudes, the number of Fabaceae genera and species, as well as Myrtaceae species, decreases (always considering tree species). However, the number of Myrtaceae genera remains constant. In the Atlantic Forest domain, floristic differentiation is mainly correlated with altitude and average duration of the dry season

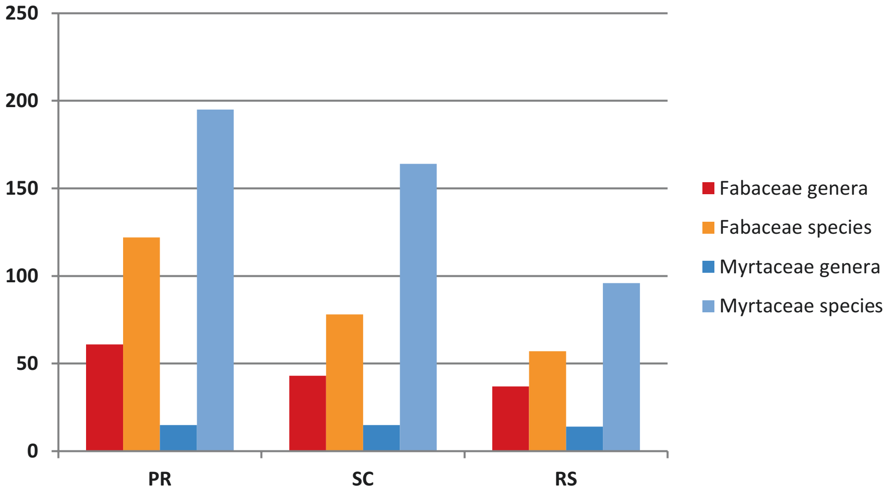

Fig. 15.1 Number of genera and species of Fabaceae and Myrtaceae trees along a latitudinal gradient in the southern region of Brazil (Paraná *PR*, Santa Catarina *SC*, and Rio Grande do Sul *RS*). (Data: Flora do Brasil 2020, only considering native trees. Accessed June 6, 2022)

(Oliveira-Filho and Fontes 2000). As a result, species abundance and richness of Fabaceae increase with the distance from the ocean, reaching its greatest importance in the seasonal forests of RS (e.g., Reitz et al. 1983), while the opposite occurs with Myrtaceae.

Evidence suggests that both in situ and ex situ events (followed by subsequent migration) shaped the patterns of diversity in the Atlantic Forest (e.g., Peres et al. 2020). Tropical elements migrated mainly from the north of the continent and temperate elements from the south (until they were isolated by the eastern SADD). The South Brazilian Plateau, with its harsh winters with regular frosts and occasional snow, represents a strong barrier to the dispersal of the tropical elements towards non-tropical latitudes in Southern Brazil (e.g., Rambo 1950, 1956, 1961). Therefore, two main routes made the process of dispersion of tropical elements possible: in the east, the strip of Atlantic coastal moist forest between the ocean and the plateau, and in the west, the Seasonal forest through the main drainages of the Plata basin—the Paraná, Paraguay, and Uruguay rivers—that begin in tropical latitudes and run in a north–south direction into subtropical–temperate latitudes (Arzamendia and Giraudo 2009).

With a large number of tropical and subtropical elements in Southern Brazil, Annonaceae, Apocynaceae, Arecaceae, Boraginaceae, Fabaceae, Euphorbiaceae, Meliaceae, Monimiaceae, Moraceae, Nyctaginaceae, Sapotaceae, and Urticaceae are typical representatives in the forests up to 500 m a.s.l., while above this line are mostly absent or underrepresented in species richness and/or number of individuals. Some tropical families are mostly restricted to the coastal moist forests, such as Chrysobalanaceae, Humiriaceae, Lecythidaceae, Magnoliaceae, and Myristicaceae, and others to the seasonal forests, such as Achatocarpaceae. There are also tropical taxa associated with very restricted formations, such as *Caryocar* (Caryocaraceae) and *Kielmeyera* (Calophyllaceae) in the *Cerrado*, and *Avicennia* (Acanthaceae), *Conocarpus*, *Laguncularia* (Combretaceae), and *Rhizophora* (Rhizophoraceae) in mangroves. On the other hand, Araucariaceae, Asteraceae, Canellaceae, Clethraceae, Cunoniaceae, Dicksoniaceae, Escalloniaceae, Podocarpaceae, Solanaceae, and Winteraceae are families well represented at elevations from 700 m a.s.l., but not only, while Anacardiaceae, Aquifoliaceae, Lauraceae, Malvaceae, Myrtaceae, Primulaceae, Rutaceae, Salicaceae, and Sapindaceae are well represented at all elevations.

Genera with high abundance and well represented in South Brazilian highlands are *Ilex* (Aquifoliaceae), *Araucaria* (Araucariaceae), *Dasyphyllum, Piptocarpha, Vernonanthura* (Asteraceae), *Monteverdia* (Celastraceae), *Clethra* (Clethraceae), *Lamanonia, Weinmannia* (Cunoniaceae), *Aiouea, Cryptocarya, Ocotea* (Lauraceae), *Miconia*, *Pleroma* (Melastomataceae), *Blepharocalyx, Eugenia, Myrceugenia, Myrcia, Myrciaria, Siphoneugena* (Myrtaceae), *Podocarpus* (Podocarpaceae), *Myrsine* (Primulaceae), *Euplassa, Roupala* (Proteaceae), *Quillaja* (Quillajaceae), *Solanum* (Solanaceae), *Symplocos* (Symplocaceae), *Laplacea* (Theaceae), and *Drimys* (Winteraceae). Mountain bamboos (*Chusquea,* Poaceae) can also be dominant in forests in the highlands, as well as species of *Merostachys* (Poaceae), also widely present in seasonal forests in Southern Brazil.

Subtropical seasonal forests have affinities with different formations along their distribution in southern Brazil, with changes in species composition primarily associated with latitude and continentality. With the increasing distance from the ocean, water availability, a key factor underlying tropical formation transitions (Dexter et al. 2018), gradually decreases, allowing an expansion of elements associated with dry formations. Important genera with high abundance and species richness in the seasonal forests are *Achatocarpus* (Achatocarpaceae), *Handroanthus* (Bignoniaceae), *Cordia* (Boraginaceae), *Actinostemon, Alchornea, Gymnanthes, Sebastiania* (Euphorbiaceae), *Anadenanthera, Apuleia, Ateleia, Copaifera, Dahlstedtia, Enterolobium, Gleditsia, Lonchocarpus, Machaerium, Muellera, Myrocarpus, Parapiptadenia, Peltophorum, Pseudalbizzia* (Fabaceae), *Nectandra, Ocotea* (Lauraceae), *Cabralea, Guarea, Trichilia* (Meliaceae), *Hennecartia* (Monimiaceae), *Ficus, Maclura, Sorocea* (Moraceae), *Campomanesia, Eugenia, Myrcianthes, Myrciaria, Plinia* (Myrtaceae), *Faramea, Palicourea, Psychotria* (Rubiaceae), *Balfourodendron, Esenbeckia, Metrodorea, Pilocarpus, Zanthoxylum* (Rutaceae), *Allophylus, Cupania, Diatenopteryx* (Sapindaceae), and *Chrysophyllum* (Sapotaceae).

In the riparian forests, scrubland and Espinal in the Pampa domain, tree species richness is low, with a small number of families and genera well adapted to the specific conditions of each type of vegetation dominating these formations. Comprising a small patch in the extreme west of Rio Grande do Sul (Espinilho State Park), Espinal (sensu Cabrera 1953) is the spatially most restricted vegetation type in Southern Brazil. It is a savanna-like formation whose trees form an impoverished group of Chacoan species, where the most representative taxa are *Schinus* (Anacardiaceae), *Aspidosperma quebracho-blanco* (Apocynaceae), *Celtis* (Cannabaceae), *Parkinsonia aculeata, Neltuma,* and *Vachelia caven* (Fabaceae). Important genera in the Pampean riparian forests and scrubland are *Astronium, Lithraea, Schinus* (Anacardiaceae), *Celtis* (Cannabaceae), *Parkinsonia, Vachelia* (Fabaceae), *Nectandra, Ocotea* (Lauraceae), *Luehea* (Malvaceae), *Eugenia, Myrcianthes, Myrciaria* (Myrtaceae), *Phytolacca* (Phytolaccaceae), *Ruprechtia* (Polygonaceae), *Quillaja* (Quillajaceae), *Condalia, Scutia* (Rhamnaceae), *Chomelia, Guettarda, Machaonia* (Rubiaceae), *Zanthoxylum* (Rutaceae), *Acanthosyris* (Santalaceae), *Chrysophyllum, Pouteria, Sideroxylon* (Sapotaceae), and *Citharexylum* (Verbenaceae).

Several widely distributed Neotropical tree species reach the Southern Brazilian forests, and most tree species that occur in the southern region are not endemic and have a wide distribution. Ranging as far as North or Central America (some including the Caribbean) to the southern limit of the Neotropical forests (Southern Brazil, NE Argentina, and some as far as Uruguay), most of these wide range species are deciduous or semideciduous, such as *Trema micrantha* (Cannabaceae), *Sapium glandulosum* (Euphorbiaceae), *Pseudalbizzia niopoides* (Fabaceae), *Ocotea puberula* (Lauraceae), *Maclura tinctoria* (Moraceae), *Myrcia splendens* (Myrtaceae), *Margaritaria nobilis* (Phyllanthaceae), *Myrsine coriacea* (Primulaceae), *Zanthoxylum caribaeum* (Rutaceae), *Casearia sylvestris* (Salicaceae), and *Boehmeria caudata* (Urticaceae). Having a wide ecological spectrum, these and other wide-range species do not necessarily have the same ecological strategies but share an extraordinary ability to adapt to different types of soils, climates, and elevational distribution. Several wide-range species can have high abundance along different forest formations and thus have been called “supertramp” species (e.g., Oliveira-Filho and Fontes 2000). On the other hand, there are few endemisms in the subtropical/temperate forests of the southern region of Brazil, most of them at the species level. The lack of endemisms at the family level and the small number at the genera level seem to show the diverse origins of the Southern Brazilian tree-flora, with southern temperate and northern tropical families and subordinate taxa both contributing to the formation of a mixed and complex flora that is largely allochthonous.

15.3 Drivers of Tree Species Richness and Composition of Forests Communities in the South Brazilian Grassland Region

Many studies have addressed the contribution of environmental and soil factors as drivers of tree species richness and composition, especially within different regions and forest types from the Atlantic Forest domain (e.g., Oliveira-Filho and Fontes 2000; Oliveira-Filho et al. 2006; Jarenkow and Budke 2009; Marques et al. 2011; Bergamin et al. 2012; Cerqueira and Martins 2015; Eisenlohr and Oliveira-Filho 2015; Marcilio-Silva et al. 2017). However, few studies have considered the forests of the Pampa regarding broad-scale vegetation patterns (Giehl and Jarenkow 2012; Oliveira-Filho et al. 2015; Neves et al. 2017; Rezende et al. 2018). Moreover, to our knowledge, no previous studies have considered only the forests that occur within the grassland-dominated landscapes in South Brazil. Paleoenvironmental studies in the Atlantic Forest and Pampa regions (Behling et al. 2004; Behling and Pillar 2007) showed large-scale dynamics between forests and grasslands since the LGM. Thus, beyond the current climatic and soil drivers, it is also important to consider past climate fluctuations to assess broad-scale vegetation patterns. Therefore, this section addresses past and current environmental drivers (climate and soil) of species richness and composition of tree communities in subtropical forests inserted in the South Brazilian grassland region.

15.3.1 Data Collection and Analysis

In order to investigate the current environmental and historical drivers of tree species richness and composition of forests located in the South Brazilian grassland region, we extracted the data from the NeoTropTree (NTT) database (Oliveira-Filho 2017; http://www.neotroptree.info). The NTT consists of a tree-species checklist

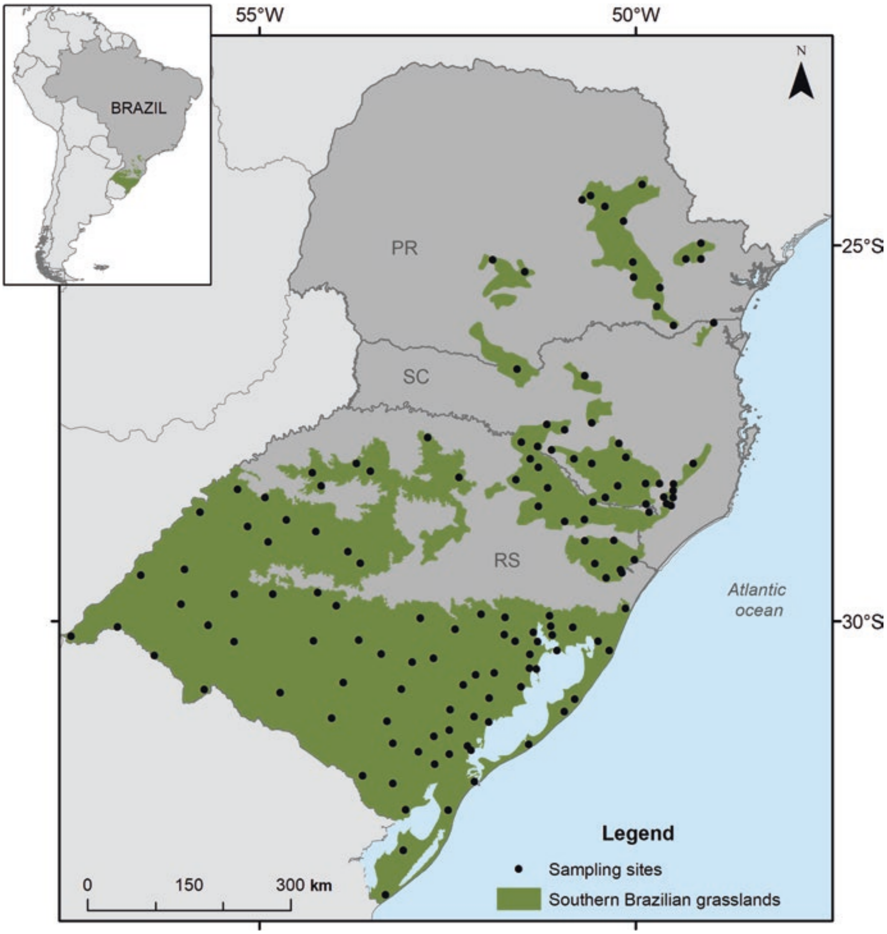

Fig. 15.2 Geographical locations of forest sites in the South Brazilian Grassland region ($n = 139$)

(woody plants >3 m in height) compiled from geo-referenced sites. We extracted forest sites occurring within the South Brazilian grassland region and excluded shrub and liana species from our analysis. The final matrix resulted in 139 sites (Fig. 15.2) with a total of 675 species (i.e., approximately 60% of total tree species richness in the southern states of Brazil). The number of species registered per site was considered the species richness of the forest community.

To assess the current environmental and historical drivers of species richness and composition of forest communities in South Brazilian Grassland region, we assembled a set of variables previously identified as important predictors of forest species richness and composition in these subtropical/temperate forests (Bergamin et al. 2012; Oliveira-Filho et al. 2015). The environmental drivers are represented by climatic and edaphic variables and comprised mean annual temperature (MAT, °C), temperature seasonality (TS, percentage measure of temperature change over the year), temperature annual range (TAR, °C), mean temperature of the coldest month (MTCM, °C), mean annual precipitation (MAP, mm/year), precipitation seasonality (PS, percentage variation in monthly precipitation totals over the year), cation exchange capacity (CEC, in mmol(c)/kg), soil potential of hydrogen (pH, pH*10), sand content (SC, in g/kg), and clay content (CC, in g/kg). Climatic variables were extracted from WorldClim (Fick and Hijmans 2017), whereas the edaphic variables were extracted from SoilGrids (Hengl et al. 2017) with a soil depth of 15 cm. In order to address the role of past climate fluctuations, we used the biome stability of South America over the last 30 kyr, measured as the frequency of each grid cell changed between forest and open vegetation (Costa et al. 2018). Thus, the lower the frequency of change between vegetation types, the greater the climate stability. Paleoclimate data and biome stability for South America are available in Carnaval et al. (2014) and Costa et al. (2018). All variables were downloaded in a spatial resolution of 5 km^2.

Previous to our analysis, we tested for redundancies between predictor variables (environmental and historical drivers) using pairwise Pearson correlation (r) and removed one variable from those pairs with $|r| > 0.7$ (Dormann et al. 2013). This led to the exclusion of MAT (positively correlated with TS), MTCM (negatively correlated with TS), and CC (negatively correlated with SC). We also applied variance inflation factor (VIF) to avoid potential issues of multicollinearity among variables, and none showed concerning levels of multicollinearity (VIF < 10). The retained variables were standardized to mean zero and unit variance to allow direct comparisons of model coefficients.

To access the drivers of species richness, we performed generalized least squares (GLS) regressions relating richness [log-transformed (Ives 2015)] with the set of retained environmental variables. We tested four different GLS models with distinct spatial autocorrelation structures (spherical, Gaussian, and exponential spatial autocorrelation) and without spatial autocorrelation, of which we selected the one with the lowest AIC value (Yuan et al. 2016; Ali and Yan 2017). The goodness of fit of the GLS model was assessed by *pseudo*-R^2 (Nakagawa et al. 2017). The GLS models were implemented using the "nlme" package (Pinheiro et al. 2016), while pseudo-R^2 was calculated with the package "piecewiseSEM" (Lefcheck 2016) of R v.4.1.3 (R Core Team 2022).

To investigate the effects of the current environmental and historical drivers of community composition, we first calculated Simpson's pairwise dissimilarity (Simpson 1943) between pairs of sites to assess the spatial turnover (Simpson 1943; Lennon et al. 2001; Baselga 2010). We then used multiple regression on distance matrices (MRM) (Goslee and Urban 2007), relating Simpson's distance matrix (response variable) with the distance matrices of environmental predictor variables (Euclidean distance matrix between pairs of sites). We also included the geographical distance between sites as a predictor variable of the community composition variation between sites. The MRM was implemented using the package "ecodist" in R (Goslee and Urban 2007) using 10,000 permutations to assess the significance of coefficients.

15.3.2 Results and Interpretation

The 675 tree species belong to 82 botanical families. Myrtaceae had the highest number of species (126), followed by Fabaceae (70), Lauraceae (47), Melastomataceae (34), and Solanaceae (29). Tree species with a higher number of records in forest sites were *Allophylus edulis* (131), followed by *Blepharocalyx salicifolius* (127), *Gymnanthes klotzschiana* (127), *Cupania vernalis* (122), and *Myrsine umbellata* (119). Forest sites with higher tree species richness are located in the northern portion of the South Brazilian grasslands, with a decrease in species richness towards the south (Fig. 15.3). The GLS model with the lowest AIC was the one that did not consider the spatial autocorrelation structure. GLS results showed that only current environmental predictors were significant, with richness being negatively related to TS, CEC, and pH but positively related to PS (Fig. 15.4). Figure 15.5 shows how tree species richness varies in relation to each significant predictor variable along the South Brazilian grasslands.

The mean pairwise compositional dissimilarity presented intermediate values (0.48 ± 0.15), ranging from 0.96 (high compositional dissimilarity) to 0.02 (low compositional dissimilarity). The MRM explained a fair amount of the variation in tree community composition ($R^2 = 0.30$, $F = 463.16$, $P < 0.01$). Results of MRM for tree community composition showed that larger differences in current environmental factors, such as TS, TAR, MAP, PS, and SC (Table 15.2), were associated with

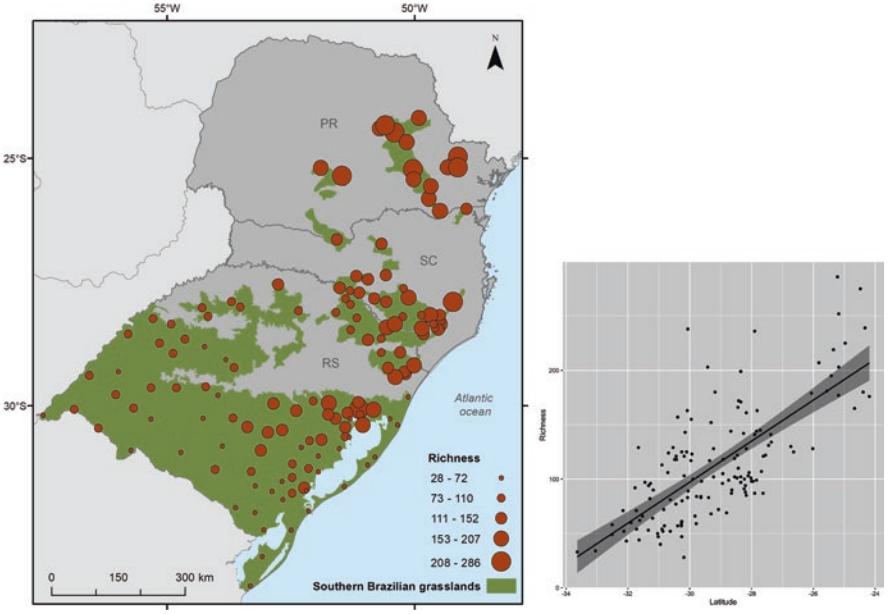

Fig. 15.3 Tree-species richness distribution per forest sites and the relationship between richness and latitude ($R^2 = 0.52$; $p < 0.01$) in the South Brazilian grassland region

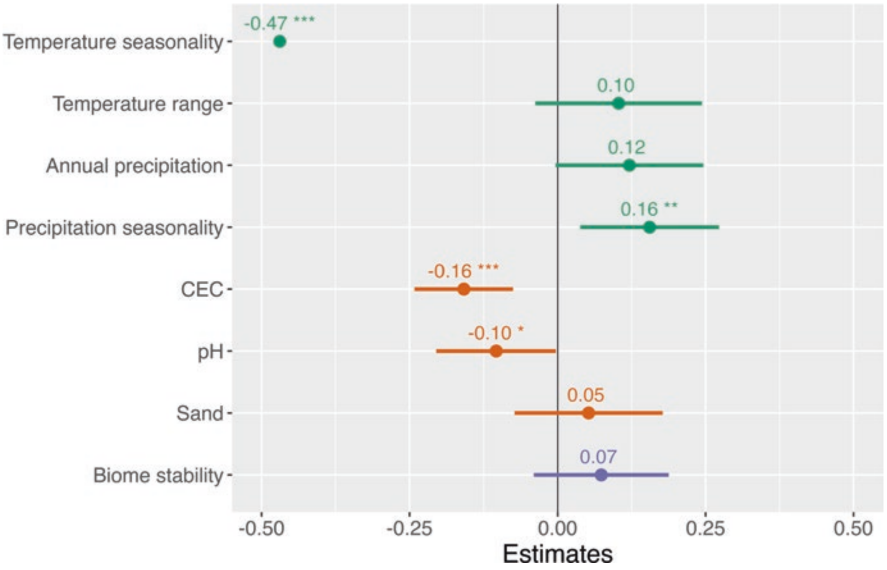

Fig. 15.4 Standardized regression coefficients of generalized least squares regression model and associated 95% confidence intervals (CI) for tree species richness in forest sites across the South Brazilian grassland region. Colors represent different sets of predictor variables. CIs that do not cross the zero baseline indicate statistically significant effects (***, $P < 0.001$, **, $P < 0.005$; *, $P < 0.05$) on tree-species richness

increased compositional dissimilarities. Biome stability was also related to the increase in tree-species compositional dissimilarity (Table 15.1). On the other hand, geographical distance did not present a relationship with tree-species compositional dissimilarities (Table 15.1).

The analyses regarding tree species richness showed that only current environmental factors (climate and soil) such as TS, PS, CEC, and pH have a relationship. The increase in TS towards the Pampa led to a decrease in species richness due to high variations in temperature along the year. In other words, the temperature extremes that occur in summer and winter seem to be the main factor (higher regression coefficient, see Fig. 15.3) that governs the differences in species richness from *Araucaria* forests in the Atlantic Forest (in the north) to seasonal forests in Pampa (in the south). Despite the low temperatures in winter, *Araucaria* forests have milder summer temperature as they are in the highland plateau. On the other hand, *Araucaria* forests presented higher levels of PS, leading to an increase in tree-species richness towards the north. It is worth mentioning that higher levels of PS do not mean water deficit periods, as the amount of precipitation is higher during the summer, and mean annual precipitation in this region is overall high (Oliveira-Filho et al. 2015).

Concerning the drivers of tree community composition in South Brazilian grassland region, we observed that both current environmental and historical factors

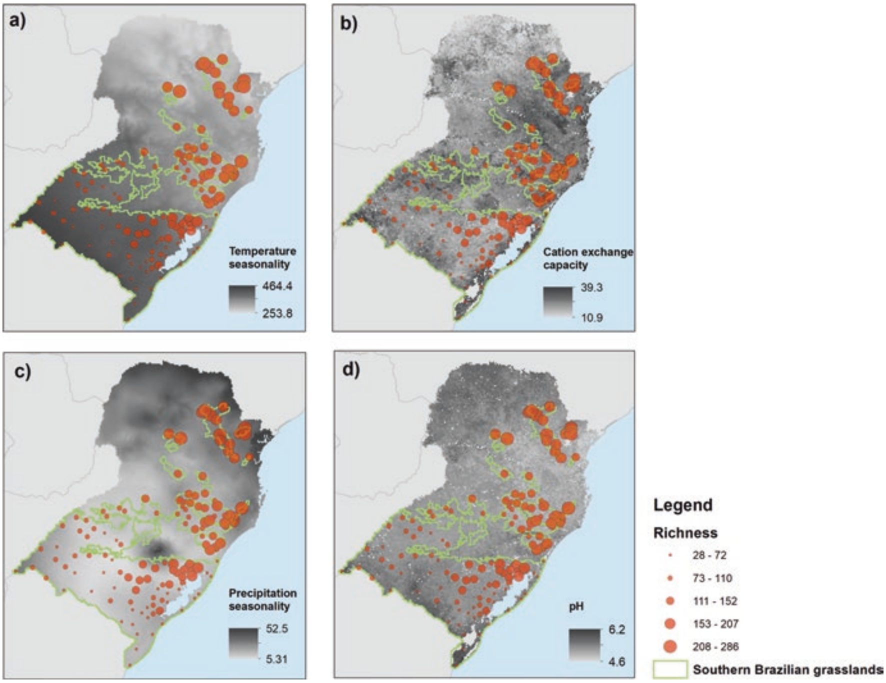

Fig. 15.5 Spatial representation of the relationship between the distribution of tree species richness in the South Brazilian grassland region in relation to each significant predictor variable: (**a**) Temperature seasonality; (**b**) Cation exchange capacity, (**c**) Precipitation seasonality, and (**d**) pH

Table 15.1 Coefficients of the multiple regression analyses on distance matrices (MRM) for different drivers (predictor variables) of tree species compositional dissimilarities in the *Campos Sulinos* region

Predictor	Coefficient	P-value
Current environmental		
TS	**0.07**	**<0.001**
TAR	**0.03**	**<0.001**
MAP	**0.02**	**<0.001**
PS	**0.03**	**<0.001**
CEC	0.01	0.08
pH	0.01	0.50
SC	**0.03**	**<0.001**
Historical		
Biome stability	**0.02**	**<0.001**
Geographical distance	−0.01	0.1

Temperature seasonality *TS*, temperature annual range *TAR*, mean annual precipitation *MAP*, precipitation seasonality *PS*, cation exchange capacity *CEC*, soil-pH *pH*, sand content *SC* influence species composition dissimilarity. Larger differences in current environmental conditions lead to high differentiation in tree species composition from *Araucaria* forests in the Atlantic Forest domain to seasonal forests in the Pampa domain, and thus a continuum of species replacement. We also found that larger differences in climate stability (historical factors) between sites influence tree-species composition variation, indicating that past climatic fluctuations played an important role in the current tree community assembly. Studies have indicated climatic stable areas with the presence of multiple small forest refugia during glaciation in the subtropical portion of Brazil (Carnaval et al. 2014; Costa et al. 2018). The multiple forest refugia scattered along the grassland matrix may have sheltered different tree-species, depending on the severity of past environmental conditions and species evolutionary adaptations. Finally, the forests in the South Brazilian grasslands, as well as the forest-grasslands mosaics, harbor high levels of biodiversity (Boldrini 1997; Bergamin et al. 2017; Rezende et al. 2018) with a gradient in species richness and shifts in community composition from *Araucaria* forests to Pampean forests.

15.4 Ecosystem Functioning and Services of Forests in the South Brazilian Grassland Region

Understanding the drivers that influence the distribution of species and vegetation types across regions is important to characterize how ecosystems function and provide different goods and services for human benefit. Physical conditions, climate variables, and biotic elements make up the ground for plant development and interactions among species and enable a number of biogeochemical cycles and ecological processes that maintain ecosystems. If functioning adequately, they provide sustainability of these ecosystems and multiple direct and indirect ecological goods that benefit humans. In this section, we describe key aspects of the functioning of forests of the South Brazilian grassland region and also discuss potential ecosystem services provided by them.

15.4.1 Ecosystem Functioning

Abiotic (e.g., temperature, precipitation, soil characteristics) and biotic factors (e.g., species composition, characteristics, and interactions) are the components that determine the functioning of ecosystems (Hooper et al. 2005). As shown in the previous section, climate is an important driver of species composition and richness, and this has direct implications for ecosystem functioning. Many patterns of ecosystem functioning found for tropical forests are similar in subtropical forests; however, some ecological processes occur at different rates due to specific climatic conditions.

Changes in temperature and precipitation influence species interactions and the rates of ecological processes, such as decomposition and productivity. Carbon sequestration and carbon stock are lower in subtropical than tropical forests due to climate characteristics (related to temperature or precipitation) that result in slower tree growth rates (Bordin et al. 2021). Tree growth is influenced by temperature and rainfall patterns, and variables such as rainfall seasonality and temperature annual range can affect tree growth and biomass stock in subtropical forests (Lucas et al. 2018; Bordin et al. 2021). Forests in the *Campos Sulinos* region therefore have slower growth rates and show lower tree size (canopy height and total stem basal area). Decomposition rates are also affected by climate variables, as they influence the activity of decomposers, but the chemistry of plant material also plays a role in the process (Aerts 1997). Additionally, water deficit and extreme events, such as frost, which are common occurrences in this region, have a high impact on ecosystem dynamics, causing species mortality and slowing growth rates (Rorato et al. 2017; Frangipani et al. 2021). Frost events can limit the establishment of species, selecting for characteristics that enable survival and growth (Rorato et al. 2017; Frangipani et al. 2021).

As previously described, climate is a determinant of species distribution across broad scales and also in the Southern Brazilian grassland region. This subtropical region is a transition between tropical and temperate climates and presents a high turnover of species: it is the southern limit of distribution for many tropical species (e.g., Rambo 1950, 1961 that are typical of the Atlantic Forest, and the northern limit of many temperate species, that come from the south (Oliveira-Filho et al. 2015). The composition of species that characterize these forests has many species with broad climatic distribution (Klipel et al. 2022 that are able to tolerate a range of climatic conditions or with vegetative adaptations to survive in this environment. These plant characteristics of leaf, stem, or root parts that influence ecological processes, i.e., their species functional traits, will determine their ecological strategies and affect the functioning of these ecosystems (Reich 2014).

Within the region of South Brazilian grasslands, both *Araucaria* and seasonal forests show ecological strategies associated with the stress-tolerant strategy, but are also influenced by different drivers. While *Araucaria* forests (found in higher elevations to the north) occur in regions with lower minimum temperatures and frost events, seasonal forests (found in the south) are affected by a larger temperature range and water deficits (Rosenfield et al. 2019). In comparison, Atlantic coastal moist forests show strategies towards the competition strategy (Rosenfield et al. 2019), which tends to occur in more productive and stable environments (Pierce et al. 2017). Species and communities with stress-tolerant strategies will show specific value ranges of functional traits, such as higher values of leaf dry matter content (LDMC) as well as low values of specific leaf area (SLA), which tend to make them more resistant to environmental conditions (Rosenfield et al. 2019), including water deficit and frost events (Reich 2014; Frangipani et al. 2021). These characteristics of acquisitive vs. conservative species, in their turn, will influence rates of ecological processes, such as decomposition and productivity (Freschet et al. 2012; Reich 2014; Garnier et al. 2004).

15.4.2 Provision of Ecosystem Services

As a result of biodiversity composition and ecosystem structure and functioning, forests provide a large array of ecosystem services, which are the ecosystem benefits (direct and indirect) that are provided to humans (MA 2005). These encompass provisioning, regulation, and cultural services: provisioning services are the wood, water, fiber, medicines, and wild fruits that are extracted and used directly from forests; regulating services are the benefits that humans have from the ecological balance provided by ecosystems, such as erosion control, climate and water regulation, flood mitigation, and pollination; and cultural services are the indirect benefits obtained from natural ecosystems, such as aesthetic beauty, cultural value, and nature interactions, that benefit human wellbeing. Tropical and subtropical forests have a large potential to provide numerous direct and indirect goods and services that benefit humans. They can provide timber and non-timber products with commercial use; regulate local/regional climate, decreasing local temperatures, and water availability or quality (Brauman et al. 2007; Rodrigues et al. 2022 GCB); increase crop pollination rates and the quality of fruits or seeds (Ricketts et al. 2004); and improve human wellbeing and quality of life through nature interactions (Díaz et al. 2018). While Brazil's subtropical forests in the *Campos Sulinos* region have a great potential for the provision of a large array of ecosystem services, studies that quantify them still are scarce.

In the category of provisioning services, these forests can provide several benefits: wood and firewood from native tree-species, such as *Cedrela fissilis* (cedro), *Gymnanthes klotzchiana* (branquilho), *Mimosa bimucronata* (maricá), *Scutia buxifolia* (coronilha), and *Vachellia caven* (espinilho), in the Pampa, and *Araucaria angustifolia* (araucária), *Eugenia uruguayensis*, *Mimosa scabrella* (bracatinga), *Myrcia lajeana*, *Myrciaria delicatula*, *Myrciaria floribunda* (camboim), *Ocotea porosa* (canela), and *Siphoneugena reitzii*, in lower and higher elevations of the Atlantic Forest (Costella et al. 2013); leaves for human consumption in the form of tea (traditional *erva-mate* from *Ilex paraguariensis* leaves); wild fruits and seeds from many native species (Brack et al. 2020). Specifically, it is worth to mention the traditionally consumed seeds from *A. angustifolia* (called *pinhão* in Portuguese) and the internationally known *Schinus terebinthifolia* (aroeira-vermelha, commercialized as Brazilian pepper) (Brack et al. 2020); and many plants with known medicinal use, such as *Bauhinia forficata* (pata-de-vaca), *Casearia sylvestris* (chá-de-bugre), *Drimys angustifolia* (casca-de-anta), *Eugenia uniflora* (pitanga), and *Monteverdia aquifolia* (espinheira-santa) (Heck et al. 2017).

In terms of regulating services, these forests can store a significant amount of carbon (Bordin et al. 2021; Pires et al. 2021) and, as common in other forested regions, contribute to the regulation of local climate and water quality near streams (Ferraz et al. 2014; Joly et al. 2019). Forests can increase water infiltration and regulate hydrological flow (Honda and Durigan 2017; Sirimarco et al. 2018), but their effect in increasing water quantity is uncertain due to high water demands and evapotranspiration. Besides carbon sequestration, riparian forests can reduce erosion and silting towards streams, improving water quality and reducing water treatment costs within a catchment (Brauman et al. 2007; Joly et al. 2019). The role of forests extends to several regulating services, including climate regulation, water balance, and soil productive capacity among others (Pires et al. 2021 Cap. 16).

Finally, when considering cultural services, the beautiful landscape mosaics of grassland and forests, such as the ones found in higher elevations of the southern part of the Atlantic Forest, are the basis for tourism, as indicated by visitation numbers of natural parks in this region (e.g., Aparados da Serra, São Joaquim and Campo Gerais National Parks, on the South Brazilian Plateau). Also, the landscape found in the Pampa, formed by rock outcrops, water bodies, and contrasting vegetation elements, is of high scenic beauty (Vieira 2014), and the forests commonly found along rivers and streams play a role in this mosaic landscape. The landscape is an important component in people's perception of the benefits obtained from natural systems. Aesthetic experience and observational interactions from forest ecosystems are shown to positively interest people (Teixeira et al. 2019) and increase their willingness to conserve natural habitats.

15.5 Changes in Forest Cover in the South Brazilian Grassland Region

Habitat loss is one of the main drivers of biodiversity loss in forest ecosystems. Overall, Brazilian forests have decreased in cover mainly caused by agriculture expansion; however, this rate varies according to the region and domain (Souza Jr et al. 2020). Besides biodiversity loss, deforestation has manifold impacts on forest ecosystems, including a decrease in habitat connectivity, an increase in edge effects, and a higher risk of fire and biological invasions (Lima et al. 2020). As described in the previous section, subtropical forests play an important role in terrestrial carbon stocks (Bordin et al. 2021), and deforestation can be extremely harmful also for ecosystem functioning and the provision of ecosystem services. Quantifying and mapping land use conversion and deforestation is essential to better target conservation efforts and guide reforestation and restoration programs.

We here present the results of a spatially explicit analysis to assess land-use and land-cover focused on changes in forest cover over a 35-year period (1985–2020) in the South Brazilian grassland region. Land-use and land-cover data were derived from MapBiomas collection 6 (Projeto MapBiomas 2022), with a spatial resolution of 30 × 30 m. Our analysis focused on changes in forest class considering the South Brazilian grassland region as a whole, as well as for the seasonal forests in the Pampa and the *Araucaria* forest in the Atlantic Forest domain separately. Then, forest cover changes were spatialized on a 20 × 20 km grid map to visualize overall patterns in forest cover changes.

15.5.1 Results and Interpretation

Our analysis showed that forest cover increased by more than 15,000 hectares from 1985 to 2020 throughout the South Brazilian grasslands (Table 15.2 and Fig. 15.6a, b). However, forest cover showed different patterns in terms of losses and gains when we compared forest coverage in the Pampa and Atlantic Forest (Table 15.2 and Fig. 15.6c). Seasonal forests in the Pampa showed an increase of 23,216 hectares in forest cover (Table 15.2), especially in the eastern part of the *Serra do Sudeste* region (Fortes 1956; Fig. 15.6a). On the other hand, *Araucaria* forests in the Atlantic Forest domain decreased by approximately 8000 hectares over the analyzed time (Table 15.2 and Fig. 15.6a).

Increases in forest cover in the South Brazilian grasslands are linked to two different processes: natural expansion over grasslands and natural regeneration after anthropic land-use abandonment. Under current climate conditions, forests are expanding over grasslands in South Brazilian grasslands in the absence of fire and livestock grazing (Pillar and Quadros 1997; Sühs et al. 2018; Müller et al. 2023, Chap. 16, this volume). For example, Oliveira and Pillar (2004) analyzed aerial photographs from 1974 to 1999 among forest-grasslands mosaics, with and without

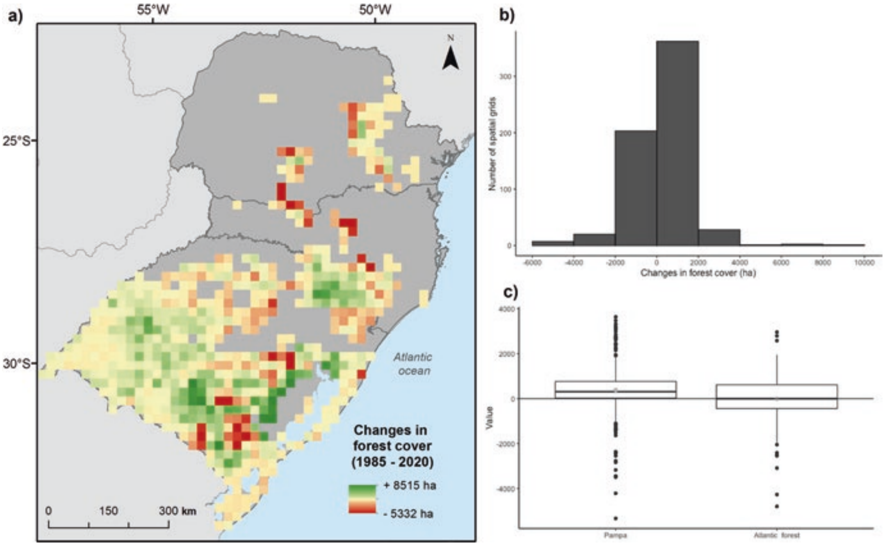

Fig. 15.6 (**a**) Spatial representation of forests cover changes in the South Brazilian grassland region from 1985 to 2020 on a 20 × 20 km grid. To better represent the original limits of South Brazilian grasslands, we removed grids with <20% of forest coverage. (**b**) Frequency of grids with forest losses and gains for the South Brazilian Grassland region. (**c**) Difference in losses and gains in forest cover between the Pampa and Atlantic Forest regions. Boxplots represent the interquartile range (IQR; box), the median (grey dot), the 1.5 × IQR interval (whiskers), and the outliers (black dots)

Table 15.2 Changes in forest cover over 35-year period (1985–2020) for the South Brazilian grasslands

	Total forest cover in 1985 (ha)	Total forest cover in 2020 (ha)	Difference between 2020 and 1985 (ha)
Atlantic forest	160,023.42	151,930.71	−8092.71
Pampa	243,378.18	266,594.49	23,216.31
South Brazilian grasslands	403,237.89	418,355.82	15,117.93

Results for the South Brazilian grasslands were divided for the two main regions (Atlantic Forest and Pampa)

management of fire and livestock grazing. They observed an increase in forest cover in the area without management, especially near forest edges. On the other hand, the area with management remained stable over time, that is, the proportion of forests and grassland remained the same. Schinestsck et al. (2019) observed a spatial pattern of forest expansion over highland grasslands in a conservation unit area. They found a transition in the proportion of forest and shrub species in relation to the distance of the forest edge (as a source of woody species for forest expansion). The closer to the forest edge, the greater the proportion of forest species, whereas the further from the forest edge, the greater the proportion of shrub species. Thus, in areas where there is a decrease in grasslands management with livestock grazing and fire, forests are expanding. Beyond the natural forest expansion over the grasslands, forest cover can also increase as a result of the abandonment of agricultural areas, allowing the natural regeneration of the forests. For example, Piffer et al. (2022) showed an increase of 3.1 Mha (million hectare) of native forest that regenerated from 1985 to 2019 in the Atlantic Forest domain as a whole. Native forest regeneration mainly occurred in areas of shifting agriculture (dynamic landscapes) and pasturelands (Piffer et al. 2022). As natural forest regeneration is considered a key component for ecosystem services restoration and biodiversity conservation, secondary-growth forests deserve more attention to support future conservation efforts in the South Brazilian grasslands.

Considering the decrease in forest cover, the main driver of deforestation is the expansion of agriculture, mainly soy plantations. For example, the area planted with soy increased by 188.5% from 2000 to 2015 in the Pampa (Capoane and Kuplich 2018). Despite the general increase in seasonal forest cover in the Pampa, our analysis indicates regions with elevated rates of forest loss. However, the proportion of deforestation was higher for the *Araucaria* forest, in the northern portion of the South Brazilian grasslands (Atlantic Forest), as the rate of forest loss was higher than the increase in forest cover over time (different from the Pampa). Although the increase in agricultural activities is mostly at the expense of natural grasslands in the South Brazilian grasslands (Overbeck et al. 2007; Andrade et al. 2016), *Araucaria* forests have also been replaced by agricultural expansion, even though this region has the highest coverage of protected areas in the South Brazilian grasslands (Overbeck et al. 2007).

Our results highlight the importance of spatial analysis focused on natural forest expansion and regeneration or deforestation due to anthropic activities to support decision-making policies for conservation and restoration planning for the South Brazilian grassland region. First, it is essential to reduce the conversion rates of forests and grasslands in the South Brazilian grassland region, especially in regions with higher levels of vegetation loss. Second, it is important to increase the number of protected areas in the region, considering mosaics of forests and grasslands, regions with lower levels of protection and with higher rates of vegetation loss. Despite its biological importance, the region remains neglected in terms of protection (Overbeck et al. 2015b). When appropriate, management in protected areas should carefully consider fire and grazing management to maintain grassland vegetation and biodiversity (Andrade et al. 2016). However, the presence of cattle inside forested areas can directly or indirectly affect tree-species establishment and survival through soil compaction, trampling, and increased seedling mortality (Vefago et al. 2019). In this case, considering that the presence of cattle only favors the dynamics of grassland formations and not the dynamics of forest regeneration, isolating some forest areas from the presence of cattle could be relevant to ensure the maintenance of regeneration processes in the medium-long term.

15.6 Concluding Remarks

Forests and grasslands historically coexist side by side in the subtropical/temperate region of Brazil, with boundaries changing over thousands of years due to climatic fluctuations. Climate change and geological events influenced the biogeographical history of South Brazilian grasslands, and forests contain trees with different biogeographical origins: Amazonian/Atlantic tropical elements, Chacoan dry elements, and Andean and Austral-Antarctic temperate elements. Thus, species from different origins contribute to the present-day rich flora.

In forests of the South Brazilian grassland region, tree-species richness decreases from *Araucaria* forests (in the Atlantic Forest) to seasonal forests (in the Pampa) as a result of current environment conditions, mainly by temperature seasonality. On the other hand, current environmental conditions and historical factors (such as biome stability) played an important role in changing species composition along the South Brazilian grassland region as a whole, for example, from the *Araucaria* forests in the highlands influenced by Andean and Austral-Antarctic elements to the seasonal forests in the south of Pampa domain influenced by Chacoan species.

Regarding ecosystem functioning and services, forests in this region have similar functions as tropical forests but at different rates due primarily to environmental filtering. This environmental filtering results in vegetation characteristics adapted to climate and soil, which, in turn, influences ecosystem functioning. Both seasonal forests in the Pampa and *Araucaria* forests have high importance for the regional water balance, carbon stocks, and maintenance of soil productive capacity, among other services. Since the conversion of natural ecosystems can change ecosystem dynamics and alter the set and amount of ecosystem benefits to humans, the conservation of these forests is essential for the preservation of biodiversity and ecosystem functioning and to the provision of ecosystem goods and services.

The contribution of these forests is particularly important in protected areas, as land use conversion inside private lands removed or degraded a large portion of these systems. When considering the low number of protected areas, especially in the Pampa (Overbeck et al. 2015b), conservation actions and planning is particularly important. Given the high and fast conversion of natural land uses in South Brazilian grassland region, actions are needed to prevent further losses of biodiversity and ecosystem functioning and to maintain the important ecosystem services provided by these systems. In addition, it is urgent to implement actions to recover and restore the mosaics of forests and grasslands that were degraded due to land use conversion. Planning such conservation and restoration efforts should surpass political boundaries to encompass all of the South Brazilian grassland region. In this context, it is essential to ensure the natural regeneration and secondary growth of forests in order to recover pre-disturbance characteristics such as biomass stock and species richness and composition.

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Chapter 16
Mechanisms and Processes Shaping Patterns of Forest-Grassland Mosaics in Southern Brazil

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16.1 Introduction

In the South Brazilian Grassland region, we often find landscapes where mosaics of forest and grassland physiognomies are intermingled, forming continuous or abrupt transitions and ecotones with manifold spatial and vertical structures. Early on naturalists have been emphatic about describing these mosaics and the associated process of forest expansion over the grasslands under the prevailing moist climate and soil types: Grasslands were considered relicts of a previous drier and colder climate now subject to substitution by forests (Lindman 1900; Rambo 1956), and not as unnatural ecosystems resultant from deforestation, as previously thought (Gautreau 2010). In the more recent past, a number of studies using different approaches including palaeoecological, soil carbon isotope, and satellite image analyses have confirmed the hypothesis of forest expansion over grasslands as a widespread phenomenon in this region (Behling 2002; Behling et al. 2004; Oliveira and Pillar 2004; Behling and

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Pillar 2007; Silva and Anand 2011; see also Behling et al. 2023, Chap. 4, this volume). Moreover, the process of forest expansion seems to have also been facilitated by human populations that managed *Araucaria* mixed forests between 1410 and 900 years before present (BP) (Reis et al. 2014; Robinson et al. 2018). The past influence of pre-Columbian civilization on forest-grassland mosaics can be expected to still affect the general woody dynamics in the region due to modifications in the spatial configuration of mosaics and in the abundance of certain species.

The presence of forest-grassland mosaics in southern Brazil and the dynamics of woody plants in grasslands result from a complex interplay of distinct drivers, including environmental, biogeographic, and landscape factors, as well as anthropogenic influences (past and current). Worldwide, studies have documented processes of woody plant encroachment, which is mainly associated with an increase of shrubs and trees in grasslands in different bioclimatic zones, particularly in regions with mean annual precipitation of at least 650 mm (Archer et al. 2017). Mesic and humid regions such as southern Brazil, where mean annual precipitation is around 1500 mm without a dry period, additionally show a gradual expansion of forest trees over the nearby grasslands. Thus, patterns of woody plant communities in the South Brazilian Grassland region arise from processes associated with both woody encroachment in and forest expansion over grassland.

Here, our aims are to (1) define forest-grassland mosaics in the light of the worldwide knowledge of transitional zones between both types of ecosystems, but focusing on and presenting vegetation patterns observed in the mosaics of the South Brazilian grassland region; (2) synthesize the current mechanisms and factors associated with the processes of forest expansion and shrub encroachment in these mosaics; and (3) propose a mechanistic model underlying the forest expansion process considering the synergies and feedbacks involved, highlighting knowledge gaps on forest-grassland dynamics for the study region.

16.2 Forest-Grassland Mosaics in the South Brazilian Grasslands: Definition and Patterns

Forest-grassland mosaics can be defined as areas with intermingled grassy and forest ecosystems that form ecotone zones with contrasting vegetation physiognomies, including the boundary itself. At the boundary (edge), the type of vegetation can vary; often,

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we find shrublands (regionally called '*vassourais*'), forming distinct physiognomies that are neither grassland nor forest. In other cases, the boundary is very abrupt, with the forest border in direct contact with grassland, or is even gradual, with forest trees entering the grassland matrix. Ecotones of forest and grasslands spread over a large part of southern Brazil (Paraná, Santa Catarina, and Rio Grande do Sul; Fig. 16.1), integrating the complex vegetation region of South Brazilian Grasslands (Overbeck et al. 2007).

Ecotones between forest and grassland in Southern Brazil can vary in terms of structural patterns at the edge and by the abundance and distribution of woody plants in the grassland part of the ecotone. These latter features are influenced by intensity and frequency of disturbances, as well as soil properties and topography. While here we are focused on woody plants, we recognize the significant

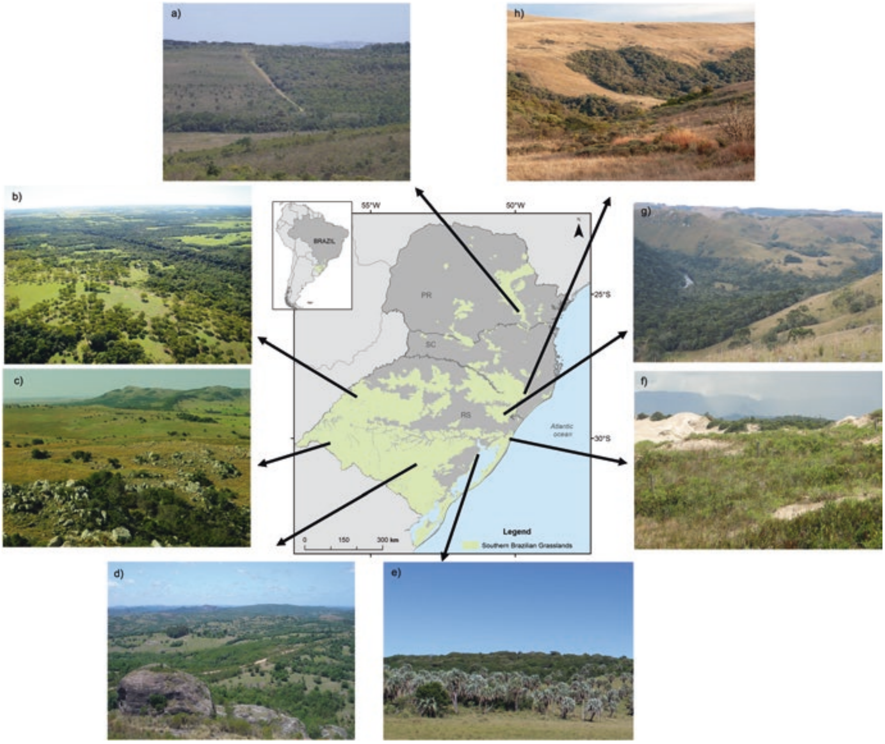

Fig. 16.1 Distribution of the South Brazilian grasslands and some examples of different types of forest-grassland ecotones: (**a**) *Araucaria* forest-grassland mosaics in Parque Estadual de Vila Velha, *Campos Gerais*, Paraná. (Photo by M. Carlucci). (**b**) Seasonal forest-grassland mosaics in the *Missões* (known regionally as "*mata de pau-ferro*"), Rio Grande do Sul. (Photo by E. Vélez). (**c**) Seasonal forest-grassland mosaics at the *Cerro do Caverá*, Rio Grande do Sul. (Photo by O. Lange). (**d**) Seasonal forest-grassland mosaics in the *Guaritas* region, Pampa, Rio Grande do Sul. (Photo by R. Bergamin); (**e**) Forest-grassland mosaics associated with *Butiazais* (*Butia* palm), in Tapes, Rio Grande do Sul. (Photo by E. Sosinski Jr.). (**f**) *Restinga* forest-grassland mosaics in the coastal region, Rio Grande do Sul. (Photo by R. Bergamin). (**g**) *Araucaria* forest-grassland mosaics in Parque Nacional de São Joaquim, Santa Catarina. (Photo by R. Sühs); (**h**) *Araucaria* forest-grassland mosaics in Parque Estadual do Tainhas, Rio Grande do Sul. (Photo by R. Bergamin)

contribution of herbaceous species to the system's heterogeneity and diversity (Andrade et al. 2023, Chap. 8, this volume). Also, herbaceous species play a crucial role in influencing ecological processes involved in grass-wood interactions (Bond 2008), both directly and indirectly, which ultimately affect the patterns of forest-grassland mosaics. The woody species present in forest-grassland ecotones can be grouped into two main categories: ***grassland shrubs or trees*** that are considered typical of grasslands due to their high frequency in such open ecosystems, and ***forest tree species*** that are representative of the nearby forest but can disperse and establish into the grassland. Examples of grassland shrubs species are the Asteraceae *Baccharis uncinella*, *B. dracunculifolia*, *B. psiadioides*, and *Acanthostyles buniifolius,* and the Sapindaceae *Dodonaea viscosa*. Examples of grassland trees are *Astronium balansae* (Anacardiaceae), *Agarista eucalyptoides* (Ericaceae), *Schinus polygama* (Anacardiaceae), *Vachellia caven* (Fabaceae)*, Xylosma schroederi* (Salicaceae), *Scutia buxifolia* (Rhamnaceae), besides palms of the genus *Butia*. Grasslands associated with *Butia* form another grassland physiognomy, the "Butiazais", a type of palm grove established on grasslands (Hoffmann et al. 2014; Sosinski et al. 2019), that even form mosaics with forest patches (Fig. 16.1), but which will not be explored here. Examples of frequent forest tree species occurring in grasslands are *Araucaria angustifolia* (Araucariaceae), *Blepharocalyx salicifolius* (Myrtaceae), *Eugenia uniflora* (Myrtaceae), *Myrceugenia euosma* (Myrtaceae), *Myrciaria cuspidata* (Myrtaceae), *Myrsine coriacea* (Primulaceae), *M. parvula* (Primulaceae), *Siphoneugena reitzii* (Myrtaceae), *Symplocos uniflora* (Symplocaceae) and *Styrax leprosus* (Styracaceae).

The forest-grasslands boundaries in the South Brazilian Grasslands region changed over time due to past climatic fluctuations (Behling et al. 2004, 2007; see also Behling et al. 2023, Chap. 4, this volume) that, together with current climate conditions and human management, shaped the patterns of vegetation distribution (Barbizan Sühs et al. 2018). The South Brazilian grasslands comprises two distinct phytogeographic regions: the Atlantic Forest in the northern portion, where different types of forest prevail, in terms of extent, over the highland grasslands, but the main forest type is the *Araucaria* forest; and the Pampa, in the southern portion of Rio Grande do Sul state, where grasslands are the dominant vegetation type, but seasonal forests are found mainly along rivers and on hillslopes (Bergamin et al. 2023, Chap. 15, this volume). The division between these two phytogeographic regions more or less corresponds to that of Parana and Pampean provinces, delimited by Cabrera and Willink (1980), and to the Atlantic Forest and Pampa biomes in the Brazilian biome classification (IBGE 2019). Forest-grassland ecotones can thus be found across heterogeneous landscapes (Fig. 16.1), and different woody species occur in the transitional zones between forest and grassland (Pillar and Quadros 1997; Oliveira-Filho et al. 2013; Gliesch-Silva 2015). Below, we provide a brief description of the main vegetation patterns of forest-grassland ecotones in distinct regions of the Atlantic Forest and the Pampa.

16.2.1 Patterns of Forest-Grassland Mosaics in the Atlantic Forest

In the Atlantic Forest region, highland grasslands form mosaics mainly with the *Araucaria* forest (Fig. 16.1a, g, h). These ecotones are strongly influenced by a cool-moist element (Oliveira-Filho et al. 2013; Rezende et al. 2016), related to Andean and Austral-Antarctic lineages (Rambo 1951a, 1953), with a great number of species restricted to this region. These biogeographic elements coexist with an 'old mountain flora' (Rambo 1953) that migrated from previously established forests from the surrounding landscape (Rambo 1961; Oliveira-Filho et al. 2013). Among the elements of Andean and Austral-Antarctic flora, we can highlight a number of tree species that colonize grasslands: *A. angustifolia, Berberis laurina, Drimys angustifolia, Podocarpus lambertii* and *Weinmannia paulliniifolia*. Forests present a high number of species from Myrtaceae and Lauraceae, and, some species, such as *Myrceugenia mesomischa, Myrceugenia miersiana, Myrcia retorta* and *Ocotea bicolor*, are restricted to this vegetation type. Many species occur in both vegetation types, forests and grasslands, such as *A. angustifolia, Myrceugenia euosma* and *Myrsine parvula*, as a result of a beginning forest expansion over the grasslands. Most woody species that are restricted to the highland grasslands are shrubs such as *Baccharis mesoneura, B. uncinella, Calea phyllolepis, Grazielia serrata* and *Gaylussacia brasiliensis.* In the northern portion, in the *Campos Gerais* region (Paraná) (Fig. 16.1a), the mosaics form a transitional zone between forests, grasslands and savannas (Overbeck et al. 2022). Vegetation patterns of this region are influenced by woody species of the Cerrado flora.

Most of the forest-grassland mosaics in the Atlantic Forest are under grazing (bovine cattle) and fire that occurs at a frequency of 2 or 3 years (Sühs et al. 2020). Therefore, most boundaries between forest and grasslands are abrupt (Oliveira and Pillar 2004; Jeske-Pieruschka et al. 2010) and few woody species occur in the grasslands. Where grazing and fire have been excluded, which happened primarily in public and private protected areas, forest expansion and shrub encroachment changed this pattern, making boundaries more subtle (Oliveira and Pillar 2004; Matte et al. 2014). Some grassland areas are subject to massive *B. uncinella* shrub encroachment, often – but not exclusively – close to the forest-grassland boundary (Dechoum et al. 2018; Schinestsck et al. 2019). Furthermore, under the absence of disturbances over longer periods, isolated trees scattered in the grassland may proliferate, shifting the landscape in terms of woodiness: tree nuclei become common in the grassland matrix (Fig. 16.2a) and tend to develop in small to large insular patches of forest known as "*capões*" (Oliveira and Pillar 2004; Duarte et al. 2006a, b; Matte et al. 2014). The colonization and establishment processes of Asteraceae shrubs and forest trees are discussed later (Fig. 16.2c, d).

Fig. 16.2 Distinct physiognomic patterns of forest-grassland mosaics in Southern Brazil. (**a**) Trees scattered in the grassland matrix, many of them are *Araucaria angustifolia*, and small forest patches known as "*capões*". (**b**) A juvenile individual of *A. angustifolia* resprouting after a fire event. (**c**) A grassland, near the boundary with forest, dominated by Asteraceae shrubs. (**d**) saplings of forest trees (e.g., *Myrsine coriacea*) colonizing a shrubby grassland. These four photos were taken in the Southern Brazilian Plateau region, in the Atlantic Forest. (**e**) High density of *A. angustifolia* in grazed grasslands in the *Serra do Sudeste* region. (**f**) Grasslands with woody encroachment, mostly of *Vachellia caven*, in the westernmost portion of Rio Grande do Sul. (**g**) Grasslands invaded by the alien species *Ulex europeus*, in the *Serra do Sudeste* region. These three photos were taken in the Pampa region. (Photos by Valério D. Pillar (**a**), Sandra C. Müller (**b**, **c**, **d**), Marcos B. Carlucci (**e**), and Fábio P. Torchelsen (**f**, **g**))

16.2.2 Patterns of Forest-Grassland Mosaics in the Pampa

The Pampa corresponds to the southernmost portion of the South Brazilian Grasslands region and the grasslands form mosaics with Seasonal forests. Here, Seasonal forests come to their southern limit and occur as riverine forests and, in a smaller scale, as forest patches on hill slopes (Oliveira-Filho et al. 2013; Carlucci et al. 2015). Inside the Pampa, there are some floristic and physiognomic differences in forest-grassland ecotones between the different physiographic regions, such as between the *Serra do Sudeste* and *Campanha* regions (Fortes 1959; Hasenack and Cordeiro 2009), mainly because of edaphic and climatic variations (see Hasenack et al. 2023b, Chap. 6, this volume).

The *Serra do Sudeste* region is characterized by grazed grasslands intermingled with small forest patches to such an extent that vegetation mapping that separates both systems at the landscape scale is complex. Because of these highly patchy landscapes, recent mapping efforts have classified it as a 'mosaic' zone (Hasenack et al. 2019) or as a 'bush grassland' (Hasenack et al. 2023a). Many tree species that are common in the forests also occur more or less isolated and with high abundance in the '*capões*', i.e., in forest patches scattered in the grassland, such as *Blepharocalyx salicifolius, Eugenia uniflora, Eugenia brasiliensis, Myrcianthes cisplatensis* and *Xylosma tweediana* (Dadalt 2010). Inside forests, in addition to the Seasonal forest elements, we can find Atlantic elements of tropical influence, which migrated from the Atlantic rain forest (e.g. *Neomitranthes gemballae* and *Ocotea silvestris*; Jurinitz and Jarenkow 2003). This is mainly observed in the northern and eastern portion of *Serra do Sudeste*, likely due to higher annual precipitation and temperature compared to other regions in the Pampa. However, these tropical elements are absent in the grasslands, likely because they are unable to colonize open areas.

This region is part of the *Escudo Cristalino Sul-Rio-Grandense*, with granitic and metamorphic rocks (Streck et al. 2008) driving topography and soil features. The soils are very often shallow, with frequent rock outcrops, as observed in the *Guarita* region (Fig. 16.1d). The edaphic limitations contribute to constrain the stature of trees and forest patches, especially in north-orientated slopes (Carlucci et al. 2015), where grasslands are often densely covered by shrubs, such as *Baccharis psiadioides* and *Dodonaea viscosa*. Moreover, in areas with higher elevations (around 400 m), there are forest patches with elements of the *Araucaria* forest as well, such as *A. angustifolia*, *Berberis laurina* and *Podocarpus lambertii* (Carlucci et al. 2011b; Oliveira-Filho et al. 2013). As mentioned earlier, these species are able to colonize grasslands, even massively, as observed with *A. angustifolia* (Fig. 16.2e) and *P. lambertii*. The species *A. angustifolia* has been detected in the Pampa since at least 1000 years ago, as evidenced by palaeopollen data (Behling et al. 2016), indicating that it was not just planted by European settlers in the region. Considering that a few other species typical of *Araucaria* forest occur in the Pampa and that the environmental suitability of *A. angustifolia* is increasingly moving southwards as a result of climate changes (Wrege et al. 2017; Bergamin et al. 2019), it is possible that the *Araucaria* forest is currently expanding its range southwards over the Pampa grasslands.

In the *Campanha* region, forest-grassland ecotones are more restricted to riverine forests and to hillsides, for example, on “testimonial hills” (isolated hills or inselbergs) of sedimentary or granitic rocks lithologies (Fávero et al. 2022) (Fig. 16.1c, d). Many of the woody species along the rivers present morphological adaptation for flood disturbances. Most grassland vegetation here is used for cattle grazing under high stocking rates (Nabinger 2002; Andrade et al. 2019) or was converted to rice fields. Therefore, forest-grassland boundaries are frequently abrupt, and often only a few individuals of forest trees occur in the grassland matrix, such as *Citharexylum montevidense, Sapium haematospermum, Schinus longifolia, Scutia buxifolia* and *Vachellia caven*. Forest-grasslands ecotones in this region are influenced by elements of the Chaco flora from Argentina (such as the species mentioned above; Vargas et al. 2022), contributing to the forest expansion over grasslands. In some regions of the *Campanha*, these floristic elements are as important as elements from the Seasonal forests (Vargas et al. 2022).

Still in the Pampa, there are additional physiognomies of large grassland areas characterized by the presence of scattered trees. Such physiognomies resemble, to a certain extent, savannas, i.e., a grass-covered system with widely spaced trees or shrubs, which also form mosaics with riverine or slope forests, as described above. Examples can be found in the *Missões* region, where individuals of the species *Astronium balansae* occur isolated in large grassland areas (Fig. 16.1b); in the westernmost portion of the Rio Grande do Sul state, the parkland areas, characterized by the presence of *Neltuma affinis*, *N. nigra* and *Vachellia caven* (Fig. 16.2f); and the *Butiazais*, the palm groves that can be found in the coastal grasslands in the Pampa (Fig. 16.1e), as well as in other grassland areas across southern Brazil (Sosinski et al. 2019).

16.3 Forest Expansion and Woody Encroachment: Mechanisms and Drivers

As we saw, grassland-forest mosaic patterns differ considerably in terms of woody species composition and abundance in the grassland portion. Such physiognomic patterns might vary (slightly or greatly) across temporal and spatial scales according to distinct mechanisms and drivers of forest expansion and woody encroachment processes, which can occur simultaneously or more or less independently. The establishment of forest woody species can, on the one hand, be a gradual process that starts with the colonization of grasslands by pioneer trees close to the edges, leading to the expansion of forest boundaries over open grassland areas (Oliveira and Pillar 2004; Müller et al. 2012a). On the other hand, nurse plants, which are isolated trees or shrubs established in grassland, can facilitate the colonization of forest woody species in two ways. First, they attract animal dispersers (primarily birds), thereby increasing seed rain beneath their crowns (Duarte et al. 2006a, 2010; Brum et al. 2010). Secondly, they improve soil conditions for more demanding forest plants (Korndörfer et al. 2015). This nucleation process promotes the formation of small forest patches within grassland sites that may then expand and develop to become well-structured forest habitats (Duarte et al. 2006a). In certain areas, rocky outcrops also serve as safe sites for the establishment of forest species and function similarly to nurse plants as nuclei of woody patches, as they also attract animals that disperse seeds and may provide protection for forest trees against fire and grazing (Carlucci et al. 2011a; Müller et al. 2012a).

In addition to the natural processes, there is also the influence of past and current human cultural management. The mosaics composed of *Araucaria* forests and grasslands are considered a domesticated landscape, shaped by pre-Columbian and contemporary societies via resource use and management (Bitencourt 2006; Reis et al. 2014). Pre-Columbian societies contributed to a fast expansion of *Araucaria* forests since 1.5 thousand years BP until the last century, with fire management being one of the factors that may have facilitated this expansion. Evidence suggests the intentional dispersal of *A. angustifolia* by these societies (Robinson et al. 2018), as the nut-like seeds ("*pinhões*") are part of the traditional diet, and the associated landscape is part of the territorial identity of the Kaingangs, among others (Reis et al. 2014). Once dispersed and established, *A. angustifolia* plants can survive fire events in grassland areas and then initiate the process of nucleation, evidencing a synergy between distinct drivers of forest expansion.

Environmental factors, disturbances, biotic interactions, anthropogenic influences as well as synergies and feedbacks between those factors are discussed in the following, considering the fundamental mechanisms and variables underlying the ecological processes of woody encroachment and forest expansion in the region.

16.3.1 Environmental Drivers

Precipitation and temperature are the two main factors used for classifying and predicting the distribution of vegetation types worldwide and at the biome and phytogeographic scales (Olson et al. 2001). In the South Brazilian Grassland region, historical increases in precipitation and temperature have enabled the expansion of forests from the northern tropical forests, including elements of both moist forests and seasonal forests, as well as from the *Araucaria* forests. Initially, this expansion occurred along river valleys and subsequently spread over the grasslands that were once the predominant vegetation type (Rambo 1951b, 1956; Behling et al. 2004). Currently, similar to other grassy ecosystems in Brazil, grasslands in the region occur in what we consider an "uncertainty climate zone" (Overbeck et al. 2007, 2022). The climate conditions, especially high precipitation well distributed over the year, without a marked dry season, are favourable to forest development (Anadón et al. 2014; Costa et al. 2018). Forests and grasslands thus co-occur at varying scales, forming mosaics, and can be considered two alternative stable states for the region (Blanco et al. 2014).

Although the overall climatic conditions allow the development of forests, there is an east-west gradient in terms of water deficit caused by the potential evapotranspiration in summer (Pillar and Quadros 1997). This gradient can constrain the establishment and growth of forest trees in grasslands, particularly those of tropical origin. Therefore, forests are predominantly found in riverine habitats or on south-facing hillsides, where local humidity conditions are more adequate for the establishment and development of forest tree species (Pillar 2003; Müller et al. 2012b; Carlucci et al. 2015). Local humidity also depends on soil properties and its ability to retain water. In regions with shallow soils, water deficit is likely to be higher, potentially restricting the establishment and growth of forest trees in comparison to grasses, forbs, and even grassland shrubs or trees of open environments. This situation may be more pronounced in some regions of the Pampa, where potential evapotranspiration in summer is higher, compared to the Atlantic Forest region, where precipitation is generally higher throughout the year. Nevertheless, despite less favourable water conditions in various areas of the Pampa, due to high evapotranspiration and shallow soils, forests still persist there (Dadalt 2010; Gliesch-Silva 2015; Vargas et al. 2022). These forests are characterized by their short stature, with trees less than 10 m tall in riverine forests (Vargas et al. 2022), as also observed in adjacent regions of Uruguay (Gautreau and Lezama 2009). This corroborates the notion that the overall climatic and edaphic conditions of the region do not preclude the existence of forests, but rather the prevailing grazing and fire management in the grasslands limit forest expansion (see details later).

In addition to water availability, it is commonly believed that grasslands generally occur in less fertile soils compared to forest ecosystems (Bond 2010). However, field studies conducted in forest-grassland mosaics suggest that differences in soil between grassland and forest patches are a result of forest colonization, rather than the cause of it (Pillar 2003; Garcia Martinez 2005; Duemig et al. 2008). Actually, it has been proposed that forest patches within grasslands in such regions may be favoured on rocky shallow soils, likely with lower nutrient and water availability. This might be attributed to synergistic relationships among deep soils, grass growth, accumulation of standing dead biomass, and fire intensity (Pillar 2003; Fidelis et al. 2010). Additionally, favourable soil conditions may increase competition between grasses and colonizing trees. The positive feedback between soil quality and grassy fuel accumulation results in higher intensity fires that may kill young trees that are still at the same height as the grassy stratum. In addition, soils with many rock outcrops may present higher density of woody species, as the rocks outcrops work as perches or refuges for animals that disperse tree species (see below). Further research is required to better understand the interplay between these feedback mechanisms and the relevance of nutrient and water availability for tree and shrub establishment in grasslands of the region.

Cold temperatures and frost can also limit the establishment of trees in open ecosystems (Hoffmann et al. 2019; Frangipani et al. 2021). Frost can be viewed as a disturbance that varies in frequency and intensity or as part of stressful environmental conditions. Either way, coping with regular frost or encountering unexpected frost events poses challenges for individuals of woody species, particularly those originating from subtropical and tropical forests attempting to colonize open grassy ecosystems (Frangipani et al. 2021). Various structures and strategies may enable plants to tolerate or mitigate frost effects, such as small, thick leaves and sprouting ability. However, when frost events occur during uncommon periods, consequences can be severe and even result in the death of adult individuals of species sensitive to frost (Hoffmann et al. 2019). Currently, the number of frost events in the South Brazilian Grassland region varies from an average of 16–18 days in Pampa to 27 days in the Atlantic Forest plateau, usually concentrated in the winter season (Alvares et al. 2018). However, due to global climate changes, there is an expected increase in extreme temperature events, heightening the uncertainty in the ability to cope with frost during the colonization process in open ecosystems. For instance, we are observing frost events in spring, such as in November 2022, contrasting with extremely hot days (around 40 °C) and periods of drought in the summer in South Brazilian regions. Consequently, the successful establishment of individual trees and further woody encroachment in grasslands may fluctuate over time.

16.3.2 Grazing and Fire Disturbances

Given that general climate and environmental conditions are more favourable to forests than grasslands in southern Brazil, disturbances play a crucial role in maintaining the coexistence of grasslands and forests in the landscape (Blanco et al. 2014). The exclusion of disturbances, such as in grasslands where management by grazing and fire has been abandoned, undoubtedly has a positive effect on woody encroachment and forest trees expansion, as woody species in general are sensitive to fire and grazing (Fig. 16.2c, d). However, some species evolved mechanisms that allow them to cope with disturbances (see Sect. 16.3.3). In addition, the effects of both grazing and fire on vegetation dynamics depend not only on the presence of the disturbance as such, but rather on the disturbance regime, i.e. the spatial extent, intensity, frequency, seasonality and return intervals of disturbance events (see Pivello et al. 2021): both fire and grazing regimes can be very diverse, thus offering windows of opportunities for recruitment of woody species even at sites with the presence of these disturbances (Fig. 16.3). Further, fire and grazing can interact, also with climatic conditions that vary among years, which can both impede or enhance woody species development.

Cattle grazing is widespread in the grassland portion of forest-grassland mosaics. Bovine cattle was introduced by Jesuits in the early seventeenth century, and cattle ranching has remained an important economic activity ever since (Overbeck et al. 2007). While the northern part of the South Brazilian Grasslands, principally in Paraná state, has experienced a shift from cattle ranching to agriculture, resulting in the conversion of most of grasslands, the landscapes in the Pampa and the eastern part of the Atlantic Forest highland region are still predominantly used for cattle

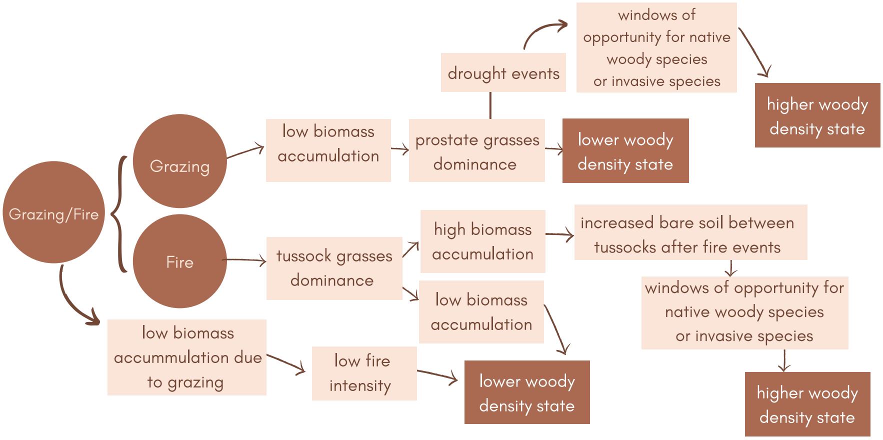

Fig. 16.3 Scheme representing different ways how disturbances and their interactions influence processes and states of woody species density ('lower' or 'higher', for simplification) in grasslands under grazing and/or fire management in forest-grasslands mosaics in Southern Brazil. See details in the text

ranching on native grasslands (Souza et al. 2020). Associated with grazing, fire is a common practice in grassland management ranching in the highland grasslands in the states of Rio Grande do Sul and Santa Catarina (Sühs et al. 2020), but its frequency is lower in the Pampa (Andrade et al. 2019). The main objective of fire is the removal of standing dead biomass of the tall tussock grasses that accumulated during the growing season and dried in winter. In the Pampa, cattle management varies in terms of intensity and frequency: continuous grazing is the most common grazing practice, but rotational grazing also may be used (Nabinger et al. 2009). These practices affect forage productivity (Boavista et al. 2019) and shrub encroachment. Tree species are scarce in these grasslands, occurring in low densities or even restricted to small patches, where unpalatable or spine-like species predominate, such as *Daphnopis racemosa*, *Scutia buxifolia*, and *Gymnanthes klotzschiana*. Due to high livestock densities in the Pampa, fire is typically infrequent and spatially discontinuous, as grass fuel is constantly consumed by cattle (Bernardi et al. 2019). Intense grazing regimes also favour prostrate species instead of tall tussock grasses, eliminating the need for burning accumulated dead biomass after winter, which is a common practice in the highland grasslands of the Atlantic Forest. However, the use and impact of fire in the Pampa grasslands vary according to local grass productivity, environmental conditions, and social factors (Paruelo et al. 2022). In some cases, landowners use fire to burn wood debris resulting from manual thinning of small woody patches, as observed in mosaic areas in the *Serra do Sudeste* region (Dadalt 2010), or even to control the encroachment of native species such as *Vachellia caven* (Fig. 16.2f) and *Dodonaea viscosa*, as well as invasive species like *Ulex europeus* (Fig. 16.2g). However, the use of fire might even contribute to the spread of these species, as seen in the case of *U. europeus* (Cordero et al. 2016), as well as likely for *V. caven* and *D. viscosa*.

In general, fire clearly retards or prevents forest expansion by killing tree seedlings, saplings, and even fire-sensitive adult trees. Fire has been recognized as a natural phenomenon caused by lightning, inclusive affecting *Araucaria* forests at least in the state of Paraná (Soares and Cordeiro 1974). Charcoal records in the highland grasslands show that fire occurrences have become more common from 7400 years BP, likely indicating the use of fire for hunting by human populations (Behling and Pillar 2007). Later, these provoked fires may have helped in maintaining grasslands by retarding forest expansion, but at the same time increasing in fire occurrences coincides with the expansion of *Araucaria* forests in the last 4000 years (Behling and Pillar 2007). The relationship between fire and forest expansion is not entirely clear. It remains uncertain whether the forest expanded despite the fires or if it actually benefited from them (Behling and Pillar 2007). This topic deserves further investigation as there is inconclusive evidence regarding the benefits of fire for the regeneration of *A. angustifolia* (Soares 1990; Souza 2021).

Under the current practices of traditional cattle raising in Atlantic Forest highland grasslands (Sühs et al. 2020), the colonization by forest tree species is likely restricted to safe sites, such as rock outcrops and isolated trees or small woody nuclei already present. However, in abandoned grasslands, the process of colonization by saplings of forest tree species increases in the first one or two decades following fire and grazing exclusion. This colonization starts close to the forest boundary and often with nurse trees or nurse rocks (Duarte et al. 2006a; Carlucci et al. 2011a). Nurse trees, particularly *A. angustifolia*, increase seed rain and ameliorate soil conditions for sapling establishment in the grassland environment (Duarte et al. 2006b; Santos et al. 2011; Korndörfer et al. 2015). The nucleation process is relevant for forest expansion because, after the exclusion of disturbances, biomass of grasslands increases considerably and vegetation will be dominated by tall tussock grasses such as *Andropogon lateralis* (Baldissera et al. 2010; Thomas et al. 2019), which can impose high competition on tree individuals (Zandavalli and Dillenburg 2015) and hamper forest expansion, at least during the first decade.

Abandoned grasslands are also prone to shrub encroachment, particularly by *B. uncinella* in the highland grasslands (Dechoum et al. 2018; Schinestsck et al. 2019). Grassland shrubs can initiate colonization shortly after abandonment or during “windows of opportunity” when soil coverage by competitive tall grasses is low. For instance, it has been observed that sporadic fire events in abandoned grasslands dominated by tall tussock grasses create opportunities for wind-dispersed species to establish in large numbers. This includes typical grassland shrubs of the Asteraceae family (*B. uncinella*) and alien species of the *Pinus* genus (*P. elliottii* and *P. taeda*), which are commonly used in tree plantations in the region. Both *B. uncinella* and *Pinus* spp. do not act as a nurse plant to the extent that *A. angustifolia* does, at least within the first 10–15 years following the exclusion of disturbances (Duarte et al. 2010; Korndörfer et al. 2015). However, as tall shrubs provide shading, pioneer trees begin to colonize the spaces in between senescent tall grasses (see Fig. 16.2d). As a result, the density of tree saplings will be higher in the proximity of forest boundaries compared to more distant areas (Müller et al. 2012a; Schinestsck et al. 2019). Moreover, these shrubs die after approximately 30 years, leaving an opportunity for a new wave of woody plant colonization, which may include typical grassland shrubs and/or forest trees depending on various environmental and spatial factors, and deserves long-term investigation. In such situations, the restoration of grassland plant communities becomes challenging or even unfeasible (Thomas et al. 2019), ultimately leading to the establishment of a stable forest or woodland community state in the short to mid- time (Blanco et al. 2014).

Differing from the Cerrado savannas, where the majority of tree species possess adaptations against fire such as thick barks, resprouting capability and even subterraneous stems (Lüttge 2007; Hoffmann et al. 2012), most tree species colonizing grasslands in southern Brazil are typical forest trees and lack typical fire-defence traits. However, some forest trees, such as *Myrciaria cuspidata, Matayba eleagnoides*, *Erythroxylum macrophyllum,* and *Myrcia palustris,* have the ability to resprout. In grasslands subjected to recurrent burns, these trees are often multi-stemmed, in contrast to their single-stemmed counterparts found within forests (Müller et al. 2007, 2012b). Tree-like palms of the genus *Butia*, including *B. eriospatha* in the highlands, *B. odorata* in the *Serra do Sudeste*, and *B. yatay* in the Pampa, have also adapted to survive moderate grassland fires as adult plants, but their saplings are unable to withstand frequent fire and intense grazing (Sosinski et al. 2019). Another species that has adapted to fire is *A. angustifolia*, whose young individuals may be killed by intense fires but that may also survive and resprout under moderate grassland fires (Fig. 16.2b). Adult *A. angustifolia* individuals exhibit good fire resistance when their stem diameter reaches 40 cm and their bark thickness measures between 5 and 10 cm (Soares 1979). Soares (1979, 1990) argues that fire plays a significant role in the dynamics of *Araucaria* forest, by reducing competition with broadleaved species in the understory, thus enabling the regeneration of the species. If this hypothesis holds true, it could explain the coincidence between the expansion of the *Araucaria* forests and the increased occurrence of fires over the past 4000 years, as shown by Behling and Pillar (2007). However, the topic requires further investigation.

In summary, even in grasslands subjected to grazing and fire, woody species can be found, particularly grassland shrubs, with varying density (Fig. 16.3). When grazing is the primary type of management and fire is rare or absent, biomass accumulation is low and prostate grasses dominate, effectively covering the soil (Jaurena et al. 2021). This leads to areas without or with low woody density. However, under drought events and high grazing pressure, these grasslands may lose their community integrity and herbaceous cover (i.e., leaving areas with bare soil), creating an opportunity for colonization by wind-dispersed woody species or even legumes that are resistant to grazing, such as the native *V. caven* and the alien *U. europeus* (Guido et al. 2023, Chap. 19, this volume). Fire may also interact here. This process may increase woody species density despite grazing, changing the community state (Fig. 16.2f, g), but still have been poorly studied in the South Brazilian Grassland region. When fire becomes the predominant disturbance factor, tussock grasses dominate in terms of coverage and height. If biomass accumulation is high (e.g., long intervals between fire events), opportunities for woody species colonization can rise after a fire due to the high proportion of bare soil between the burnt tussocks. Under moderate grazing pressure and/or a combination of both fire and grazing, a double stratum of grasses is often observed, with prostrate species intermingled with tussocks. As tussocks are being rejected by animals, they accumulate dead biomass during the winter period, also as a consequence of frost, which leads to increased fire intensity. Consequently, grasslands generally have a lower woody density state. The density of forest tree species in these grasslands is thus primarily influenced by safe sites availability, spatial heterogeneity, forest distance, and landscape context, as well as other factors discussed in the subsequent subsections.

16.3.3 Biotic Drivers

Biotic drivers here considered include interactions and plant traits associated with processes of dispersal and establishment of shrubs and trees in grasslands. The process of tree colonization and nucleation of forest patches in grasslands strongly relies on the efficiency of seed dispersal from forests to open sites. Commonly, in woody plant communities exposed to high rainfall levels, seed dispersal is mostly promoted by animals (Howe and Smallwood 1982; Herrera 2002) with behavioural habits and habitat preferences that determine seed fate (Nathan and Muller-Landau 2000; Jordano et al. 2007). In the *Araucaria* forests, the relative importance of seed dispersal by animals increases southwards, which is related to a gradual reduction of rainfall seasonality as distance from northern seasonal forests increases (Duarte et al. 2009). Thus, in South Brazilian grasslands, the initial colonization of grasslands by forest tree species mediated by nurse plants is mostly promoted by animal dispersers (Duarte et al. 2006a, 2007). Woody plants established in grasslands, especially individuals of *A. angustifolia*, attract frugivorous birds that use them as perches for resting and/or foraging activities, which increases seed rain beneath them. More developed forest patches situated within a grassland matrix show a higher proportion of frugivorous birds when compared to continuous forests and edges (Hartz et al. 2012). Moreover, increased seed removal levels by vertebrates have also been observed in large forest patches (Brum et al. 2010), suggesting positive feedbacks between the development of woody patches and recruitment of animal populations, which likely affect patch dynamics.

The colonization of grassland sites by forest species also involves coping with resource limitations (e.g., water or nutrient stress) and the incidence of frosts, and also the need to tolerate or avoid disturbances (see above). Trees established as isolated individuals in grasslands improve microclimatic conditions and the availability of soil resources, facilitating the establishment of other forest species beneath their crowns (Korndörfer et al. 2015). Indeed, symbiotic interactions with forest trees colonizing grassland sites may enhance nutrient uptake (Silva and Anand 2011). Interestingly, Korndörfer et al. (2015) found that individuals of *A. angustifolia* have a significantly higher effect on the availability of key nutrients, such as N and P, than *B. uncinella*, a common shrub species found in grasslands of the Atlantic Forest biome. Further, Al levels beneath *Araucaria* trees are lower than beneath

Baccharis crowns. These results strongly support the role of *A. angustifolia* as a nurse plant in expanding forest patches, first established as isolated individuals and then as small nuclei within the grassland matrix (Fig. 16.2a).

The tree species able to disperse (mostly zoochoric species) and establish in grasslands must possess traits that enable them to tolerate fire and/or avoid being grazed, as these disturbances are common in grassland ecosystems (see above), as well as tolerate frost. Resprouting ability is crucial under fire regimes (Müller et al. 2007) and frost (Frangipani et al. 2021), but thick barks can also provide protection (Hoffmann et al. 2012). Under grazing regimes, traits such as resprouting ability, spiny leaves or stems, and unpalatable leaves confer higher tree performance within grasslands (Gautreau and Lezama 2009; Dadalt 2010; Carlucci et al. 2012). Hence, trees that successfully overcome the establishment phase within grasslands often share similar leaf traits, such as small leaf area, low specific leaf area (SLA), and high dry matter content (LDMC) (Klipel et al. 2023). These traits improve their ability to tolerate frost events as young saplings and potential water restrictions resulting from exposure to high solar radiation, cold temperatures, and wind in open ecosystems (Frangipani et al. 2021).

In addition to the nucleation process, the expansion of forest elements over grasslands also occurs near the boundary, sometimes associated with shrub encroachment (Müller et al. 2012a). The habitat conditions at the forest boundary are favourable for the establishment of pioneer trees, which may grow faster than late secondary species and surpass the critical height threshold between fire intervals (Hoffmann and Franco 2003; Hoffmann et al. 2012). As these trees grow, fire intensity decreases locally due to increased humidity under their crown and decreased grass fuel accumulation (C4 grasses diminish their cover in the shade), creating improved conditions for other tree species to establish and gradually expand the forest edge over the grasslands. These conditions and the higher humidity in forests usually stop the spread of fire at the boundary, allowing the gradual expansion of forest patches (Müller et al. 2012b). The nurse plant effect also plays a role in this edge expansion, as most saplings are found beneath trees established near the boundary between grassland and forest (Carlucci et al. 2011c). Furthermore, the colonization of forest trees within grasslands is also observed beneath the crown of massive shrubs that encroach when grassland management is reduced or absent (Fig. 16.2c, d) (Schinestsck et al. 2019).

The establishment of tree species within grasslands is mediated by animal dispersal, as mentioned earlier. However, the establishment of most shrubs is not reliant on animal dispersal, as most species are typically wind-dispersed, especially within the Asteraceae family (Müller et al. 2012b). Dispersal and competition with grassy species are fundamental processes associated with dense shrubby patterns in grasslands observed in sites with less favourable soil conditions. In areas with shallow or poor soils, for instance, competition with grass species is less intense and there is more space for the establishment of small-sized wind-dispersed seeds. Such shrub species also possess traits that enable them to grow fast, resprout after fire events, resist high radiation and low water conditions and even tolerate frosts. Common traits observed in these species include very small leaves, multi-stemming, sucker roots and underground organs with buds (Müller et al. 2007; Fidelis et al. 2010).

16.3.4 Anthropogenic Factors

In order to properly understand ecological phenomena, it is important not to overlook processes that have been ongoing for decades or centuries (Vellend et al. 2013). Human activities have played a significant role in shaping the appearance and functioning of landscapes and ecosystems for millennia (Bürgi and Gimmi 2007), and landscapes without human influence are purely hypothetical (Denevan 1992; Vitousek et al. 1997; Clement and Junqueira 2010; Levis et al. 2017). The field of historical ecology aims to comprehend human-environment interactions and their consequences on the formation of both contemporary and past cultures and landscapes (Balée 2006). From this perspective, humans are considered a keystone species within a multispecies context, as they construct niches, domesticate species and landscapes and disturb ecosystems, thereby integrating environmental dynamics and potentially increasing species richness and landscape diversity (Balée and Erickson 2006; Clement et al. 2015; Zeder 2016; Vellend 2017; Albuquerque et al. 2018). In South America, landscapes domesticated by pre-Columbian societies can be found in a wide range of environments, in both tropical (e.g., Denevan 2003; Erickson 2006; Clement et al. 2015; Levis et al. 2017) and subtropical (e.g., Reis et al. 2014) regions. Despite the interconnectedness between human cultural practices and species-environment interactions, our understanding of how these elements affect species diversity, composition and distribution (Reis et al. 2014; Boivin et al. 2016), as well as landscapes, remains limited. Thus, in order to understand the current dynamics of the landscape, it is crucial to recognize that past events, often spanning millennia, have shaped ecosystems worldwide (Swetnam et al. 1999; Reis et al. 2014).

In southern Brazil, human hunter-gatherer societies arrived around 12,000 years BP, and successive peoples occupied the highlands, within the *Araucaria* forest region (Noelli 2000; Bueno et al. 2013). These societies relied on a variety of forest resources, including wood, fruits and seeds, and promoted the dispersal of some species (Noelli 2000; Pereira Cruz et al. 2020), including *A. angustifolia* itself (Bitencourt 2006; Reis et al. 2014). The use and management of forest resources intensified around 2500 years BP, with the arrival of agricultural societies from different traditions (Tupi and Macro-Jê) (Noelli 2000), and fire became more frequent in these landscapes (Behling et al. 2004). Contrary to the conventional notion of sedentarism, around 1300- and 1414-years BP, the subsistence economy was based on mobility, which allowed for the use and management of forest resources integrated with agricultural practices involving the cultivation and consumption of manioc (*Manihot esculenta*), beans (*Phaseolus* sp.), yams (*Dioscorea* sp.), maize (*Zea mays*) and squash (*Cucurbita* sp.) (Corteletti et al. 2015). The fact that mobility was a central aspect of the Jê peoples' way of life during this period likely contributed to the formation of forest-grassland mosaics at the landscape scale. Thus, it can be argued that this represents a cultural landscape (Reis et al. 2014), resulting from a process of landscape domestication (Clement and Junqueira 2010), as human actions over time have enhanced productivity and safety for the inhabitants.

Following the arrival of European settlers around 500 years BP, wars and diseases devastated most of the traditional peoples, settlements, cultures and landscapes (Noelli 2000; Reis et al. 2014). The collapse of these populations likely led to a drastic reduction in the frequency of fire management, potentially contributing to forest expansion (Jeske-Pieruschka et al. 2010). This process then likely was slowed down by the arrival of domestic cattle from the seventeenth century on. Currently, in the highlands where extensive cattle raising is the main activity, farmers regularly use fire as a tool to promote the regrowth of foraging grasses to feed the cattle (Nabinger et al. 2000). As already seen, these management practices contribute to limit forest expansion and maintain grasslands (Pillar 2003; Overbeck et al. 2007; Sühs et al. 2020), and, together with protected areas, can ensure high landscape diversity in these regions (Barbizan Sühs et al. 2018). The traditional management practices employed by local farmers in highland grasslands have been passed down for centuries, constituting a legacy landscape. Although the origins of these practices are still uncertain, they may have roots in the techniques used by pre-Columbian societies, such as the *Kaingang* and *Xokleng* peoples, who employed fire management in grasslands. The traditional management involves burning winter-dried grasslands at the end of winter/or the beginning of spring (August and September). Fire is implemented every 2–3 years to stimulate grassland vegetation regrowth to be grazed by domestic cattle, which is raised in an extensive system with approximately 4 free-ranging animals per 10 hectare of grassland (Sühs et al. 2020). The traditional management fires are characterized by low intensity and height, primarily consuming the dried biomass of the grasslands, mostly at the top layer. The practice rarely burns the entire grassland area, resulting in large patches of unburned grasslands that potentially serve as refugia for animals. Moreover, since dry biomass is kept at low levels, fire affects only grasslands and shrubs at the forest edge and does not burn forest interiors. The presence of cattle, which use the forest for protection and foraging, likely contributes to prevent fire within the forest by creating trails and compacting litter, effectively impeding the spread of fire.

16.4 A Mechanistic Model: Synergies and Feedbacks in Processes and Patterns of Forest-Grassland Mosaics

We propose a comprehensive mechanistic model that illustrates the main interactions between the fundamental drivers and distinct factors or variables, which collectively create synergistic positive or negative feedback loops that influence the presence and density of woody plants within the grasslands in forest-grassland mosaics in southern Brazil (Fig. 16.4). While most of the details of each factor

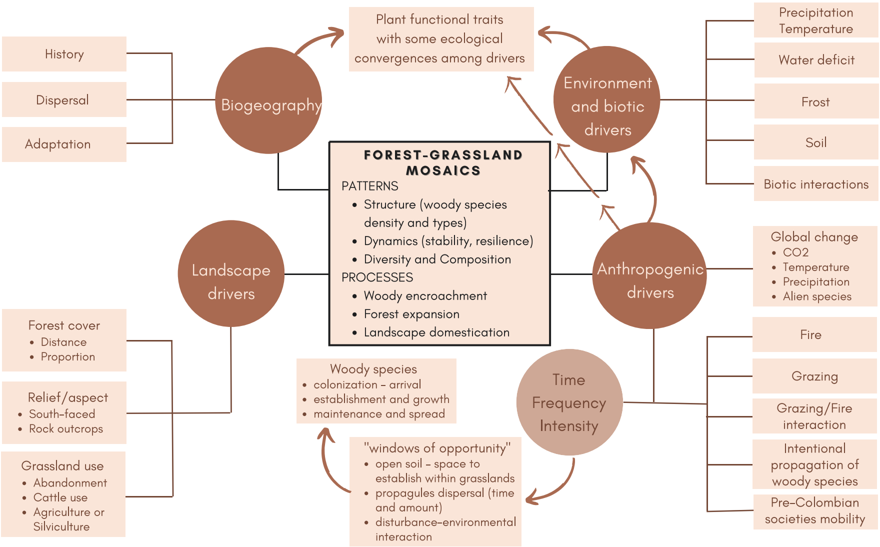

Fig. 16.4 General mechanistic scheme of woody species colonization and density dynamics over the grasslands in South-Brazilian forest-grassland mosaics, including main drivers of patterns and processes. Details are discussed across the text

underlying mechanisms and processes have been already discussed, we will now emphasize some interconnections between different categories explored earlier.

Among the environmental drivers, precipitation and temperature are worldwide determinants of forest-grassland mosaics, and they have been crucial in determining the expansion of forests in Southern Brazil over the last 8000 years, increasing the coverage of *Araucaria* forests and seasonal forests in the entire South Brazilian Grassland region. However, regional and local patterns of forest patch distribution within grasslands are linked to landscape features such as relief, aspect and forest coverage, as well as other environmental conditions such as soil water deficit and frost intensity. Both water deficit and frost occurrence are expected to change under global climate changes, which might affect forest expansion rate and shrub encroachment in grasslands of forest-grassland mosaics. While frost invariably hinders the establishment of trees in grasslands, droughts can indirectly promote the establishment of shrubs by reducing herbaceous coverage and creating spots of open soils that offer an opportunity for wind-dispersed shrubs to establish. In addition, plant traits and biotic interactions, both considering plant-plant interactions (grass-woody plants competition and facilitation through nurse plants, for example) and animal-plant interactions (seed dispersion) drive the patterns of woody species establishment and density in grassland areas, especially for tree species that come from the forest. The biogeographic history of woody species that occur in these mosaic regions influences plant attributes, which in turn affect their performance under different conditions and management contexts. These plant traits may be closely linked to the species' origins or even exhibit convergent evolution among species that have developed similar trait states to adapt to distinct factors. For example, small, leathery leaves, spine-like stems and the ability to resprout are trait states of woody plants to cope with either climatic constraints, such as high solar radiation, cold temperatures, frost and water deficit, as well as with anthropogenic disturbances, such as cattle grazing and fire.

Furthermore, the forest coverage in the landscape and the distance to forest boundaries are important factors in determining the density of trees within the grasslands and the rate at which forests expand (Oliveira and Pillar 2004; Schinestsck et al. 2019). The rate of forest expansion in the region, however, has been very slow since at least the Late Holocene, with only around 100 m over the past few millennia (Silva and Anand 2011), as shown by fossil pollen records (Behling 2002) and soil carbon isotopes (Duemig et al. 2008; Silva and Anand 2011). This may be attributed to the scarcity of tree species propagules away from the forest boundaries and the constraints associated with establishing trees in open ecosystem conditions, including environmental limitations and disturbances. As we have discussed earlier, the density of forest trees in grasslands is largely influenced by the distance of larger forest patches, presence of animal dispersers, presence of rock outcrops (safe sites), relief and aspect, which result in forest nucleation and patches been predominantly observed on south-facing reliefs and areas with rock outcrops. However, pre-Columbian civilizations also influenced the dispersion of tree species in the region, particularly *A. angustifolia*, an important nurse plant for other tree species to establish in grasslands. Consequently, we can observe north-facing slopes with patches of *Araucaria* forests in the highland grassland region (Robinson et al. 2018). Abundance and distribution of *A. angustifolia* was overall increased across the South Brazilian Grassland region due to the influence of these civilizations, further affecting the process of forest expansion due to its nucleation role. Then, the arrival of Europeans in the region, with land-use conversion to agriculture or silviculture and the widespread use of cattle raising in remaining natural grasslands up to today, slowed down and strongly affected woody encroachment and forest expansion processes. Past and current forest expansion and woody encroachment in forest-grassland mosaics regions are thus a result of the sum of ecological processes mediated by natural and anthropogenic drivers.

Although we are proposing this mechanistic model to synthesize the patterns and processes of woody encroachment and tree expansion in forest-grasslands mosaics in Southern Brazil, there are still important gaps in our knowledge, particularly regarding empirical evidence across the region as a whole, but also considering mechanisms of plant performance under distinct contexts. Few studies have focused on understanding the relative influence of different levels of disturbances and their interactions, such as between grazing pressure and timing of fire events, and about the magnitude of competition between grasses and woody plants at sites with distinct soil properties in terms of fertility and water availability. Furthermore, global climate change may interact with ecological processes in unexpected ways. For instance, while there is an expectation that C3-woody plants will have an advantage in growth rate by higher CO_2 levels in the atmosphere (Blanco et al. 2014), the effect of increased CO_2 on grassy-woody plant coexistence in grasslands remains uncertain, especially given that these grasslands are composed of a mix of C4 and C3 grass species. It has been shown for grassland ecosystems further to the south, in Uruguay (Fernández et al. 2014, 2019), that grass species from the two functional groups respond differently to the presence of shrubs: C3 species can be positively associated with the presence of shrub, in contrast to C4 grasses. The topic certainly deserves investigation in South Brazilian grasslands, and ideally over climatic gradients, as well. Additionally, the expected increase in extreme weather events due to global climate change may counteract the potential advantage of woody species due to the increased CO_2, likely reducing their performance in grasslands, particularly forest trees, due to the increasing frequency of droughts and out-of-season frost events. These are just a few study topics that require further attention towards a better understanding of patterns and processes of woody encroachment and forest expansion in South Brazilian forest-grassland mosaics.

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Part V
Conservation of the *Campos Sulinos*

Chapter 17
Beyond Protected Areas: Conservation of South Brazilian Grasslands

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17.1 Introduction

The conservation efforts concerning the *Campos Sulinos* have been entangled for decades in a discussion between protecting grasslands and protecting forest ecosystems, the two main ecosystem types that coexist in this transitional region. Forests in the region, part of the Atlantic Forest complex, have suffered large reductions in area in the past (Fonseca 1985), while loss of grasslands is a more recent process. Implementation of conservation strategies and actions in the region is not keeping pace with land use change and degradation, resulting in alarming risks to biodiversity: the Pampa region, the southern part of the *Campos Sulin*os, for instance, is the region with the highest conservation risk index of all Brazilian regions (Overbeck et al. 2015). Clearly, much higher conservation efforts are necessary to protect natural ecosystems in southern Brazil and their biodiversity. Current conservation efforts are also not keeping pace with global agreements on biodiversity conservation, such

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as the Aichi targets or the more recent Kunming-Montreal Global Biodiversity Framework which was adopted in 2022.

The field of biodiversity conservation has experienced many modifications over the past decades (e.g., Kareiva and Marvier 2012). One important change is the implicit recognition of the role of humans and their needs in conservation discussions and strategy development. While biodiversity remains a central focus of conservation efforts, it is now accompanied by the consideration of the various ecosystem services that are vital to human populations and by the recognition of the underlying processes that guarantee these services and thus also must be targeted by conservation action. This shift is driven by a growing understanding of how land degradation impacts the ecosystem services provided by natural ecosystems and, consequently, human societies (e.g., Díaz et al. 2015; Joly et al. 2019). Indeed, today we recognise that different crises, such as the climate crisis and the biodiversity crisis, are interconnected and cannot be addressed separately (Farber 2015). However, attention on global biodiversity degradation remains focused on forests, while open ecosystems remain neglected. This is also true for the *Campos Sulinos* that are not much considered in the context of the Brazilian and global conservation debate (e.g., Krob et al. 2021).

Recent research has led to improved knowledge on the effects of human action on biodiversity of the *Campos Sulinos*. Land use change in the region leads to habitat loss, but also has negative effects on biodiversity of grassland remnants (Staude et al. 2018, 2021) and other adjacent ecosystems (Dala-Corte et al. 2016, Fig. 17.1). Associated degradation processes, such as invasions by alien species, further reduce native biodiversity (see Guido et al. 2023, Chap. 19, this volume). Effects of land use change and degradation on other conservation assets, for instance on the many ecosystem services grasslands provide (Pillar et al. 2015), have been less documented in the region, despite its high potential, for example, for carbon storage in the soil (see Tornquist et al. 2023, Chap. 14, this volume). While transformation of natural ecosystems into agricultural landscapes leads to increased provisioning of some services (e.g., food production), it is well known that other ecosystem services are reduced (Zhang et al. 2007). This is also true for intensification of grassland use that will lead to higher provisioning of some services, but losses in others (e.g., Bullock et al. 2011).

Beyond their consideration in protected areas, South Brazilian grasslands face another challenge: the lack of adequate strategies for their protection. Conservation efforts in the region have traditionally focused on forests, and only recently a debate on how best to protect grasslands has been initiated. Divergent ideas regarding conservation requirements of grasslands and the most effective approaches to achieve them have emerged (Pillar and Vélez 2010; Luza et al. 2014; Overbeck et al. 2016; Carlucci et al. 2016). In this context, grazing and fire, in particular, have become polemical topics and remain misunderstood by some participants in the conservation debate (Baggio et al. 2021; Pivello et al. 2021). A more objective debate on how best to conserve grasslands, in protected areas and on private property, is necessary.

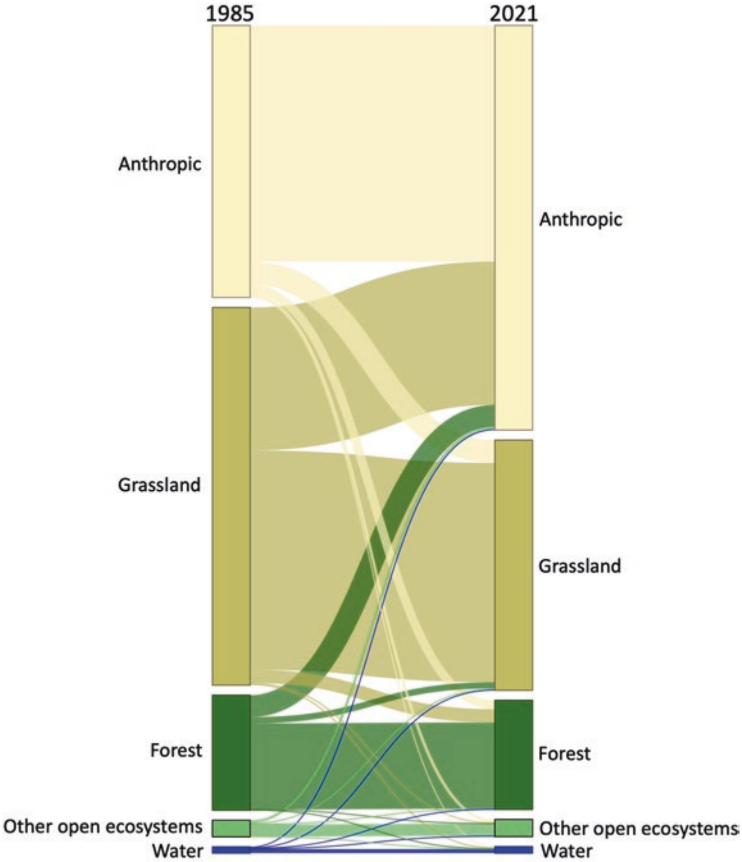

Fig. 17.1 Land use change in the *Campos Sulinos* region between 1985 and 2021. The definition of the *Campos Sulinos* region follows Overbeck et al. (2023, Chap. 1, this volume). Clearly, grasslands are the ecosystem type that is most affected by land use change in the recent past (Data: Mapbiomas 2023). (Figure: E. Vélez-Martin)

Here, we wish to contribute to the ongoing debate on conservation in the *Campos Sulinos* region by addressing three main topics. We start with a synthesis of the current level of protection in the region, focusing on protected areas as the main component of area-based conservation efforts. Then, we discuss the potential of Legal Reserves, a key conservation instrument in Brazilian law, to complement the protected area network. Finally, we discuss the need for adequate management practices for conservation of grasslands. We are concerned here with the conservation of grasslands and grassland biodiversity across space and time, and we do not address more specific conservation problems such as the impact of invasive species, discussed by Guido et al. 2023, Chap. 19, this volume.

17.2 Protected Areas as Key Elements of Conservation: How Well Are Grasslands in the *Campos Sulinos* Region Protected?

Protected areas (PAs) are a fundamental cornerstone of biodiversity conservation (Maxwell et al. 2020). Networks of PAs constitute a minimum reserve of preserved regional biodiversity, ecosystem processes and cultural memory. They also serve as sites for environmental education, as well as a genetic reservoir for restoration (e.g., by their role in seed sourcing). The Brazilian System of Protected Areas (*Sistema Nacional de Unidades de Conservação da Natureza* – SNUC, in Portuguese) regulates the implementation and management of PAs in the country. Created in 2000 through Law 9,985, the SNUC provides unified and standardised rules and management strategies with the main common objective of nature conservation. It consists of 12 categories to be implemented at federal, state and municipal levels of government administration, which are grouped into two main types: (i) strict protection areas, which are reserved to protect biodiversity, allowing only indirect use under specific conditions defined by law; and (ii) sustainable use areas, which have the primary focus on nature conservation but allows the sustainable use of natural resources. For a description of all 12 PA categories considered in the SNUC, refer to Table 17.1.

Currently, Brazil has 18% of its land under some level of protection (Vieira et al. 2019). This is a substantial percentage when compared with neighbouring countries and even wealthier nations, allowing Brazil to meet the requirements of Aichi Biodiversity Target 11, which calls for the conservation of at least 17% of terrestrial and inland water areas by 2020. If indigenous lands, *quilombola* territories, and military areas are also considered, the protected area coverage in Brazil rises to 29.4% (Vieira et al. 2019), which is close to the 30% target set by the Kunming-Montreal Global Biodiversity Framework.

However, it is important to recognise that not all types of vegetation found in Brazil are equally protected. Most of the land (70%) within PAs is found within the limits of the Amazon region, followed by the Cerrado and Atlantic Forest regions, while grassy ecosystems that dominate the landscapes in the Pantanal and Pampa regions receive the least protection (Overbeck et al. 2015; Vieira et al. 2019). Previous analyses of PAs and land use in the *Campos Sulinos* region, or parts thereof, have highlighted insufficient protection of grasslands (Overbeck et al. 2015; Oliveira et al. 2017), as well as biases in the spatial distribution of PAs (Vieira et al. 2019). Furthermore, considerable portions of PAs in the *Campos Sulinos* are under severe anthropic impacts, such as agricultural or forestry use, or are degraded in various ways (Ribeiro et al. 2021).

Here, we provide updated information on the coverage of federal, state and municipal PAs in southern Brazil and their current contribution to conserving the grassland ecosystems in the region. We used data from Brazil's National Registry of Conservation Units (MMA 2023), based on data available in March 2023, with additional information from state and municipal units obtained from environmental

Table 17.1 Types of Protected Areas under SNUC that are found within Southern Brazil. Activities: scientific research (SCI RES); public visitation (PUB VIS); education and environmental interpretation (EDU ENV INT); mineral exploitation (MIN EXP); permanence of traditional communities, that already lived in the area when the protected area was created, is allowed (TRAD COMM); hunting (HUNT); commercial exploitation of timber (TBR); natural resource extraction by traditional populations living on the land (NAT RES EXT); sustainable natural resources exploitation (SUST USE); land use conversion to agriculture (LULCC)

Protected Areas (PAs) categories	Land ownership	Main goal and apparent restriction by habitat type	Activities	IUCN management category (IUCN WCPA 2020)	Forest, grassland, agriculture(%)[a]	Area within Southern Brazil (ha, %) (MMA 2023)	Example in the *Campos Sulinos* region
Strict Protection (32.3% of the total area of PAs in southern Brazil)							
Ecological Station	Public	Nature conservation and scientific research. Management and restoration practices are allowed	Allowed with restrictions: SCI RES, EDU ENV INT Prohibited: PUB VIS	Ia – Strict Nature Reserve	0.7%, 0.3%, <0.1%	Atlantic Forest: 25,141 ha, Pampa: 32,806 ha, Total: 57,947 ha (2%)	Taim Ecological Station
Biological Reserve	Public	Nature conservation with minimal human interference. Management and restoration practices are allowed.	Allowed with restrictions: SCI RES, EDU ENV INT Prohibited: PUB VIS	Ia – Strict Nature Reserve	2.5%, <0.1%, 0.2%	Atlantic Forest: 77,632 ha, Pampa: 9,959 ha, Total: 87,591 ha (3%)	São Donato Biological Reserve
National/State/ Municipal Park	Public	Conservation of natural areas with ecological relevance or beautiful scenery. No mention of allowed management and restoration practices	Allowed with restrictions: SCI RES, EDU ENV INT, PUB VIS	II – National Park	18.6%, 1.6%, 0.9%	Cerrado: 887 ha, Atlantic Forest: 667,589 ha, Pampa: 70,253 ha, Total: 738,729 ha (25.6%)	Campos Gerais National Park, Itapuã State Park
Natural Monument	Public or private	Conservation of rare and unique natural areas or of great scenic beauty	Allowed with restrictions: SCI RES, EDU ENV INT, PUB VIS, TRAD COMM	III – Natural Monument or Feature	0.1%, 0%, <0.1%	Atlantic Forest: 4,723 ha, Pampa: 0 ha, Total: 4,723 ha (0.2%)	Palanquinho Natural Monument

(continued)

Table 17.1 (continued)

Protected Areas (PAs) categories	Land ownership	Main goal and apparent restriction by habitat type	Activities	IUCN management category (IUCN WCPA 2020)	Forest, grassland, agriculture(%)[a]	Area within Southern Brazil (ha, %) (MMA 2023)	Example in the *Campos Sulinos* region
Wildlife Refuge Area	Public or private	Conservation of the natural environment to ensure species maintenance and breeding	Allowed with restrictions: SCI RES, EDU ENV INT, PUB VIS, TRAD COMM	III – Natural Monument or Feature	0.7%, 0.2%, 0.2%	Atlantic Forest: 32,181 ha, Pampa: 9,008 ha, Total: 41,188 ha (1.4%)	Banhado do Maçarico Wildlife Refuge Area
Sustainable use (67.7% of the total area of PAs in southern Brazil)							
Environmental Protection Area	Public or private	Conservation and sustainable use of extensive areas of special relevance to human well being	Allowed: SCI RES, PUB VIS	V – Protected landscape	24.7%, 13.1%, 16.4%	Cerrado: 184,087 ha, Atlantic Forest: 1,262,027 ha, Pampa: 446,124 ha, Total: 1,892,239 ha (65.6%)	Ibirapuitã environmental protection area
Area of Relevant Ecological Interest	Public or private	Maintenance of small areas of natural ecosystems with local or regional importance	Allowed: SCI RES, PUB VIS	IV – Habitat/ Species Management Area	0.3%,<0.1%, 0.1%	Atlantic Forest: 12,016 ha, Pampa: 2,992 ha, Total: 15,008 ha (0.5%)	Morro Ferrabraz Area of Relevant Ecological Interest
National/State Forest	Public or private	Multiple use of forest resources and scientific research	Allowed: SCI RES, PUB VIS, TRAD COMM	VI – Protected Areas with Sustainable Use of Natural Resources	0.3%, <0.1%, <0.1%	Atlantic Forest: 15,462 ha, Pampa: 0 ha, Total: 15,462 ha (0.51%)	São Francisco de Paula National Forest

Extractive reserves	Public	Protection of areas inhabited by traditional populations which depend on the extraction of natural resources, ensuring their sustainable use	Allowed with restrictions: SCI RES, PUB VIS, TBR, NAT RES EXT, TRAD COMM Prohibited: HUNT, MIN EXP	VI – Protected Areas with Sustainable Use of Natural Resources	<0.1%, 0%, <0.1%	Atlantic Forest: 782 ha, Pampa: 0 ha, Total: 782 ha (0.03%)	Pirajubaé Marine Extractive reserves
Sustainable Development Reserve	Public	Nature conservation and ensuring traditional human populations well-being, as well as value and conserve traditional knowledge and traditional techniques of sustainable use of natural resources	Allowed: SCI RES, PUB VIS, TRAD COMM, SUST USE, LULCC	VI – Protected Areas with Sustainable Use of Natural Resources	<0.1%, 0%, <0.1%	Atlantic Forest: 345 ha, Pampa: 0 ha, Total: 345 ha (0.01%)	Ilha do Morro do Amaral Sustainable Development Reserve
Fauna Reserve	Public	Technical-scientific studies on sustainable management of faunal resources	Allowed: SCI RES Allowed with restrictions: PUB VIS Prohibited: HUNT	IV – Habitat/ Species Management Area	0%, 0%, 0%	Atlantic Forest: 0 ha, Pampa: 0 ha, Total: 0 ha (0%)	–
Private reserves	Private	Conserve biological diversity.	Allowed: SCI RES, EDU ENV INT, PUB VIS	IV – Habitat/ Species Management Area	0.8%, 0.1%, <0.1%	Atlantic Forest: 25,196 ha, Pampa: 3,851 ha, Total: 29,047 ha (1%)	RPPN Estadual Barba Negra, RPPN Pró-Mata.

The current data on land cover and land use were obtained from MapBiomas (2023), and the area and distribution of PAs follow the National Registry of Conservation Units in Brazil (MMA 2023)

[a]These are the overall three main land use classes, but they do not represent the total percentage shown in parentheses after strict protection and sustainable use items (see also Table 17.2). In addition to forest, grassland and agriculture, there are other classes such as other open ecosystems, beach and dune, water, other anthropic uses and a small portion of not evaluated areas

agencies. All area calculations included all terrestrial PAs located partially or entirely within the boundaries of southern Brazil (i.e., Rio Grande do Sul, Santa Catarina and Paraná states). Overlaps between PAs, if any, have been excluded to avoid double counting. Data on extension of PAs were used to extract land use and land cover data provided by MapBiomas collection 7.1 (2023) for the year 2020.

Only 5% of the territory of southern Brazil is currently protected by PAs, and the distribution of PAs across the region is highly unbalanced (Fig. 17.2). In terms of area, most PAs are located in the state of Paraná (59%), in the northern portion of the region, followed by Rio Grande do Sul and Santa Catarina states, accounting for 26% and 15%, respectively. This spatial concentration of PAs highlights significant gaps in biodiversity conservation throughout the region, as it fails to adequately protect all existing ecosystem types, including various types of grasslands (Andrade et al. 2019) and forests (Oliveira-Filho et al. 2013). Furthermore, the current PAs system in southern Brazil is clearly biased towards the conservation of forest ecosystems, neglecting the protection of grasslands and other non-forest ecosystems (Table 17.1 and 17.2). This bias is concerning given the current disproportionate threat faced by grassland ecosystems. Between 1985 and 2021, grasslands in southern Brazil have lost 3,761,751 ha (a decline of 33% since 1985), while forests have lost 994,183 ha (a loss of 6% since 1985) by conversion to agriculture and other anthropic uses (MapBiomas 2023). Furthermore, the composition of vegetation types within the PAs does not reflect the proportion of regional forest and grassland remnants that existed in 1985, which were 27% and 20%, respectively. Currently, within PAs, the main land cover classes are forest, agriculture and grasslands, accounting for 49%, 18% and 15%, respectively (Table 17.2). Quite obviously, the presence of large areas of agriculture is not the most appropriate use when the main objective of an area is conservation of the natural vegetation. The high proportion of agriculture is associated with the category of sustainable use PAs and illustrates the challenges with implementing PAs in the region (Ribeiro et al. 2021).

Considering the total area covered by the 317 recorded PAs in southern Brazil, 68% belong to the sustainable use type, while 32% are strict protection areas (Fig. 17.2). Forest ecosystems are evenly distributed between sustainable use and strict protection PAs in terms of area. However, most grassland ecosystems are found within sustainable use areas (Table 17.2). On the one hand, this allocation appears appropriate as in sustainable use areas, landowners can continue with land management practices that are compatible with the conservation goals of the respective area. This is the case of extensive cattle grazing, which allows for the integration of biodiversity conservation and economic benefits for the local population (e.g., Baggio et al. 2021). On the other hand, grasslands within sustainable use areas can be converted to another land use if legally authorised, making these areas more vulnerable. Considering the necessity of grasslands to be under adequate disturbance or management regimes (see below, in Sect. 17.4), it is important to emphasise that even in PAs designated as strict protection, management should be allowed when it contributes to grassland conservation. The management approach applied will depend on the conservation goals and objectives of the specific area. Despite the concentration of grassland in the sustainable use PAs, they still occupy a smaller

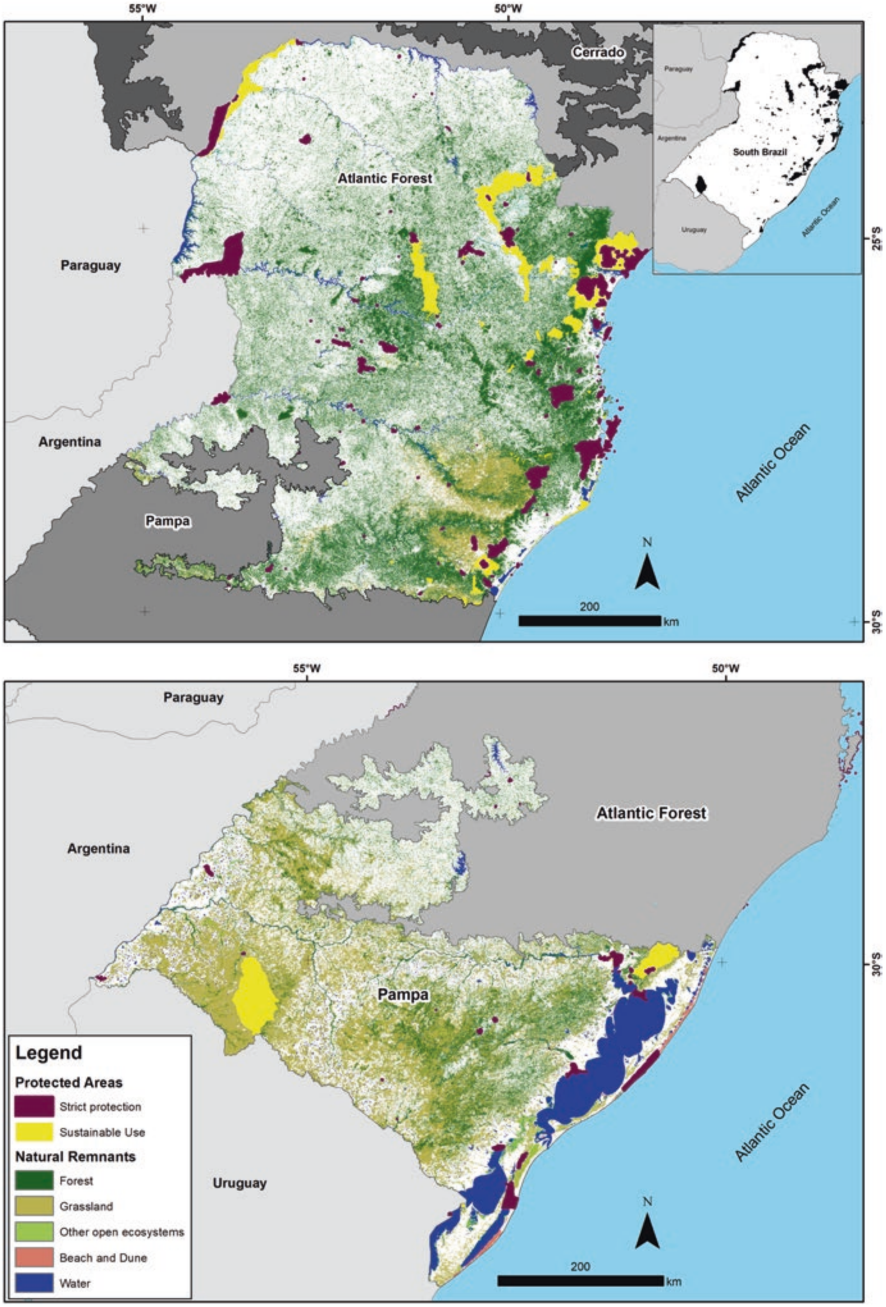

Fig. 17.2 Map of Federal/State/Municipal Strict and Sustainable Use Protected Areas (PAs) in southern Brazil. The black-and-white map on the upper right corner shows all PAs, while the other two other maps zoom in on the Atlantic Forest and Pampa regions. The current data on land cover and land use were obtained from MapBiomas (2023), and the area and distribution of PAs follow the National Registry of Conservation Units in Brazil (MMA 2023)

Table 17.2 Distribution of habitat type within federal, state and municipal PAs in southern Brazil. There are 317 protected areas in the South of Brazil (two of them at least partially included within its territory)

Protected Areas *(area in hectare)*	Forest	Grassland	Other open ecosystems	Beach and Dune	Water	Agriculture	Other anthropic uses	NA	Total
All Strict Protection areas	**653,381**	**62,536**	**103,152**	**13,563**	**36,328**	**38,447**	**19,556**	**1,672**	**928,637**
Ecological Station	21,059	9,559	15,326	487	8,986	987	1,445	65	**57,914**
Monumento Natural	3,707	54	0	1	522	300	92	0	**4,676**
State Park	130,417	10,878	11,246	711	8,243	10,373	6,617	135	**178,621**
National Park	395,292	33,598	64,525	12,141	17,901	13,714	6,048	1,447	**544,666**
Municipal Park	10,759	419	264	217	177	1,281	894	7	**14,017**
Wildlife Refuge Area	19,121	6,718	5,110	1	101	6,119	3,990	9	**41,169**
Biological Reserve	73,028	1,310	6,682	6	398	5,674	469	8	**87,574**
All Sustainable Use areas	**753,373**	**379,730**	**81,013**	**4,393**	**93,585**	**475,845**	**158,324**	**6,408**	**1,952,671**
Area of Relevant Ecological Interest	9,361	826	312	6	1,618	1,781	774	331	**15,010**
State Forest	167	0	0	0	0	22	101	0	**290**
National Forest	7,434	41	616	0	65	267	6,742	4	**15,169**
Sustainable Development Reserve	251	0	2	0	33	54	6	0	**346**
Extractive Reserves	668	0	4	0	52	20	33	1	**778**
Private Reserves	24,108	1,526	325	217	436	535	1,874	2	**29,023**
Environmental Protection Area	711,384	377,336	79,754	4,170	91,381	473,165	148,794	6,070	**1,892,054**
Total	**1,406,755**	**442,266**	**184,165**	**17,956**	**129,913**	**514,293**	**177,881**	**8,080**	**2,881,308**
%	48.8	15.3	6.4	0.6	4.5	17.8	6.2	0.3	**100**

The current data on land cover and land use were obtained from MapBiomas (2023), and area and distribution of PAs follow the National Registry of Conservation Units in Brazil (MMA 2023) total area compared with forests. In some of the sustainable use PA categories, no grassland areas are at all present. This is reasonable for categories such as National/State/Municipal Forest, where the main objective is to apply and develop methods, technology and research on the sustainable multiple uses of forest resources. However, one might question why there is no similar category specifically dedicated to grasslands.

Only one PA category, the Environmental Protection Areas (which falls under the sustainable use type), represents 66% of the entire area covered by PAs in the region (Table 17.2). Sustainable use PAs have been preferred by decision-makers because they do not require expropriation or displacement of landowners. The importance of community-based efforts in conserving and managing these PAs, such as through livestock ranching on native grassland (see Baggio et al. 2021) is undeniable. However, the high percentage of agriculture, particularly soybean production and other anthropic uses in these areas (18% and 6% respectively, as shown in Table 17.2) indicates divergence from the commitment to biodiversity conservation at the landscape scale. These numbers reflect the absence of strong administration that regulates recommended and permitted uses within PAs, as well as the lack of extension activities and outreach programmes that support sustainable and profitable solutions integrating direct benefits (such as food, medicine and forage production) and indirect benefits (such as education, recreation and tourism) derived from biodiversity. Such measures should aim to maintain biodiversity and provide ecosystem services. Clearly, there is a need to advance the implementation of effective management strategies in PAs in southern Brazil.

Given the low coverage of protected areas in the region, only 5% across southern Brazil and even less in specific regions such as the Pampa (IBGE 2019), the designation of additional PAs should be a priority of public policy. However, Brazil's PAs currently face ongoing challenges, including downgrading, resizing and degazetting both across the country as a whole (Bernard et al. 2014), and specifically in the southern region (Golden Kroner et al. 2019; for more information, see the PADDD tracker initiative with updated data available at https://padddbrasil.org.br/). Under these circumstances, designating new PAs over larger areas seems quite unrealistic. Nevertheless, some regions in southern Brazil, such as the Serra do Sudeste, are of particular interest for conservation due to their significant number of endemic species and comparatively less severe land use change (MMA 2018).

If the objective of the PAs is to conserve regional biodiversity, it is important to ensure that they actually contain a large proportion of this biodiversity. For the *Campos Sulinos* region, covered mainly by grassy ecosystems, some studies evaluating changes in species composition over space (beta diversity patterns) are available, particularly for trees (Saraiva et al. 2018; Bergamin et al. 2017) and grassland plant communities (Menezes et al. 2022). Both forests and grasslands exhibit high turnover, indicating high compositional differences across space. In the case of grasslands (Menezes et al. 2022), the mean proportion of the turnover component (beta diversity) was 95%, while for forests (Bergamin et al. 2017), it was 86%. These results clearly indicate that if the goal is to protect the diversity of grassland plants and forest trees, the spatial configuration of the PA system needs to cover the region better than the current one, and the implementation of other area-based conservation efforts (i.e. *Reserva Legal*; see Sect. 17.3) must be fulfilled. Specifically considering new PAs, their establishment must prioritise regions that have not been previously considered. Needless to say that in practice the creation or improvement of protected area networks requires more information than just beta diversity in the vegetation of specific habitat types such as grassland or forest, as in the examples above. Other habitat types and species groups need to be considered as well. This information is used, for instance, in the development of priority areas for conservation by the Brazilian Ministry of the Environment, with the last update in 2018.[1]

17.3 Legal Reserves and Areas of Permanent Protection

Apart from its protected area network (as discussed above), Brazilian legislation mandates two additional types of area-based conservation efforts that can play a significant role in the conservation of biodiversity and ecological processes: the Legal Reserve (RL; *Reserva Legal*, in Portuguese) and Areas of Permanent Protection (APP; *Área de Preservação Permanente*, in Portuguese). These mechanisms, regulated by the Native Vegetation Protection Law (NVPL), primarily aim to restrict and regulate the use of natural vegetation in rural private properties, thus outside the Brazilian System of Protected Areas (SNUC) (Brancalion et al. 2016). They are crucial for preserving the remnants of native vegetation and ensuring the restoration of degraded areas. APPs protect riparian margins, steep slopes and other sensitive habitats aiming to preserve water resources, protect soil integrity, maintain geologic stability, safeguard biodiversity, facilitate gene flow and enhance the well-being of human populations (Brancalion et al. 2016).

The RL, on the other hand, is an area where native vegetation must be preserved and, according to the NVPL, it must include a fixed percentage of the property, which varies across different regions of Brazil. In the Amazon region,[2] the RL must cover 80% of the property in forests and 35% in savanna; elsewhere in the country (including grassland vegetation areas in southern Brazil), the RL must cover 20% irrespective of vegetation type. Economic activities can take place within the RL, as long as the native vegetation cover is maintained. If the native vegetation has been previously destroyed, it must be restored, with some exceptions depending on the date of conversion and size of the property. The primary objective of the RL is to conserve biodiversity and ecosystem services, and promote sustainable use (see Metzger et al. 2019) within landscapes with anthropic use.

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[1] Maps are available for download at: https://www.gov.br/mma/pt-br/assuntos/servicosambientais/ecossistemas-1/conservacao-1/areas-prioritarias/2a-atualizacao-das-areas-prioritarias-para-conservacao-da-biodiversidade-2018

[2] Brazil's Amazonia Legal, a sociogeographic region in Brazil, which encompasses the nine Brazilian states that include the Amazon forest region, and also includes adjacent ecosystems.

In theory, both APPs and RLs provide an excellent and complementary opportunity to preserve native vegetation and other components of native biodiversity across a significant portion of the landscape, including the potential to connect larger natural areas protected under the SNUC. The estimated total area of non-forest ecosystems in the Brazilian Pampa that could be protected by RLs and APPs was approximately 2.9 million hectares in 2014 (Overbeck et al. 2015), with about 90% of this area being grasslands. Even considering a 20% conversion since then, there is still a potential to protect around 2,3 million hectares of native grassland remnants through RLs and APPs in the Brazilian Pampa. This area is about 38 times larger than the current distribution of grasslands and associated open ecosystems in strictly protected areas, and six times larger when including the sustainable use PAs under SNUC in the Pampa (Table 17.3).

However, in practice, the implementation of RLs has been plagued with problems, mostly due to political pressures. The agribusiness sector has strongly opposed the RLs (Metzger et al. 2019), and some weakening of the instrument was successfully approved through the 2012 Native Vegetation Protection Law (Santiago et al. 2017), which replaced the Forest Code as the main legislation of biodiversity conservation in Brazil. Additional state regulations could help environmental legislation achieve its most important objectives with greater effectiveness and clarity. Unfortunately, besides incomplete implementation, there have been attempts to undermine important concepts in legislation (see Box 17.1). An example in the *Campos Sulinos* region is Decree No. 52,431/2015 of the state of Rio Grande do Sul, later incorporated into the state environmental code (Law No. 15,434/2020, which establishes the bizarre concept of “suppression of natural vegetation by livestock grazing”, in an attempt to mischaracterise those areas currently with grassland remnants, and no longer require their conservation within Legal Reserves. According to the federal NVPL (Article 68), landowners who suppressed native vegetation when there was no RL requirement, are exempt from meeting the RL percentage requirement. The elaboration of a legal concept which considers grazing as leading to the suppression of native grassland vegetation contradicts all scientific evidence that clearly shows the contrary. Instead of causing suppression, grazing has played an important role in the history of *Campos Sulinos* grasslands and in maintaining species-rich natural grassland communities (e.g., Ferreira et al. 2020; Baggio et al. 2021).

Implementation problems also extend to the Rural Environmental Registry (*Cadastro Ambiental Rural* – CAR in Portuguese). CAR is a self-declaratory system for online registration of rural properties, which allows the assessment of their spatial limits and environmental compliance regarding the NVPL (Brancalion et al. 2016). All landowners are required to declare the limits of native vegetation remnants, as well as identify APPs and the RL within the boundaries of the property. If native vegetation remnants are non-existent or below the legal requirement to fill in the RL, they must restore the degraded area or compensate elsewhere using the available mechanisms under the NVPL. The CAR has the potential to support compliance and facilitate control, monitoring and enforcement actions. However, its implementation across Brazil is far below expectation. While progress in the state

Table 17.3 Total area (in hectares) of protected area for strict and sustainable use in the Pampa, Atlantic Forest and Cerrado regions in the South of Brazil

Pampa									
Protected Areas *(area in hectare)*	Forest	Grassland	Other open ecosystems	Beach and Dune	Water	Agriculture	Other anthropic uses	NA	Total
Strict Protection	13,640	25,408	35,159	12,731	22,091	7,538	5,454	10	**122,026**
Sustainable Use	47,744	331,049	11,458	223	9,381	46,262	6,358	496	**452,968**
Total	**61,383**	**356,457**	**46,617**	**12,954**	**31,472**	**53,800**	**11,812**	**506**	**574,994**
Atlantic Forest									
Protected Areas *(area in hectare)*	Forest	Grassland	Other open ecosystems	Beach and Dune	Water	Agriculture	Other anthropic uses	NA	Total
Strict Protection	639,364	36,892	67,908	833	14,233	30,732	14,097	1,661	**807,265**
Sustainable Use	660,182	39,340	54,506	4,170	84,099	355,407	112,045	5,866	**1,315,829**
Total	**1,299,546**	**76,232**	**122,414**	**5,002**	**98,332**	**386,139**	**126,142**	**7,527**	**2,123,094**
Cerrado									
Protected Areas *(area in hectare)*	Forest	Grassland	Other open ecosystems	Beach and Dune	Water	Agriculture	Other anthropic uses	NA	Total
Strict Protection	378	237	85	0	3	178	6	0	**887**
Sustainable Use	45,448	9,341	15,049	0	106	74,176	39,921	46	**184,087**
Total	**45,826**	**9,577**	**15,134**	**0**	**109**	**74,354**	**39,927**	**46**	**184,974**

The current data on land cover and land use were obtained from MapBiomas (2023), and the area and distribution of PAs follow the National Registry of Conservation Units in Brazil (MMA 2023) of Paraná can be considered adequate, it is insufficient in Santa Catarina and nonexistent in Rio Grande do Sul, which encompasses the largest portion of grassland ecosystems (Chiavari et al. 2021).

In summary, the full implementation of the RL has the potential to make a significant contribution to grassland conservation at the scale of millions of hectares. However, its current impact is severely limited due to implementation problems. Furthermore, even if implemented properly, there are some limitations to biodiversity conservation. For instance, in those cases where it is necessary to restore the native vegetation within RL, the allowance of up to 50% exotic species (Santiago et al. 2017) can restrict the full contribution to biodiversity conservation in practice.

Box 17.1 Most Significant Advances in Legislation for the Conservation of Brazilian Grasslands

Brazilian legislation has long neglected grassy ecosystems, such as grassland and savanna, even though they originally covered 27% of the territory. Here, we present a timeline on the main national and regional legislation that directly impacts conservation and management of *Campos Sulinos*.

1934 – The Brazilian Forest Code (Decree No. 23,793) was the first piece of legislation focused on conservation of natural ecosystems. Grassy ecosystems are hardly mentioned, except for the regulation of intentional application of fire to grassland vegetation.

1965 – Federal law No. 4,771 replaced the Decree from 1934, also under the term Forest Code. It established the obligation of landowners to protect 20% of their private properties with forest cover, known as Legal Reserves (*Reserva Legal*, in Portuguese). As much as its importance is unquestionable, it was biased in favour of the conservation of forests. The management of grassy ecosystems was not contemplated by this law and the use of fire as a management tool, which had long been applied by traditional communities, was criminalised.

2001 – Executive order No. 2,166-67 amended the Forest Code and extended the obligation of Legal Reserve to any vegetation type, which included grasslands.

2004 – The Pampa is recognised by the Brazilian Institute of Geography and Statistics (IBGE) as one of the six official Brazilian biomes.

2005 – Amendment No. 48/2005 to the state legislation of Rio Grande do Sul aims to value and preserve the cultural practices, genetic variability and diversity of species in the Pampa region. However, applicability is limited.

2006 – The Atlantic Forest Law (Law No. 11,428/2006) – which imposed strong restrictions to native vegetation suppression – recognised the highland grasslands of South Brazilian as part of the Atlantic Forest vegetation type. Insufficient law enforcement is still a bottleneck for the effective conservation of highland grasslands. There is no similar law for the Pampa grasslands.

2008 – Decree No. 6,660 amends the Atlantic Forest Law and recognises livestock grazing as a sustainable management practice in the highland grassland.

2010 – National Environmental Council (CONAMA) resolution No. 423/2010 describes successional stages of the highland grasslands and establishes criteria for authorising the suppression of vegetation. The Pampa grasslands do not have equivalent regulations.

2012 – The Forest Code is replaced by the Native Vegetation Protection Law (NVPL; Law No. 12,651/2012) which explicitly incorporates non-forest ecosystems in the Brazilian conservation agenda. Despite this, the term ‘Forest Code’ continues to be widely used, even in publications by government agencies, which is misleading and fails to effectively educate the general public about the protection of all native vegetation, regardless of whether it is classified as forest or non-forest. Alongside the land use restrictions present in the previous Forest Code, the NVPL introduced additional provisions such as the requirement for authorisation of native vegetation suppression and the establishment of the Rural Environmental Registry.

2014 – State (Rio Grande do Sul – RS) Decree No. 51,882 establishes an index of grassland conservation in the state of Rio Grande do Sul. This index serves as a basis for providing financial incentives to landowners who contribute to the conservation of biodiversity and ecosystem services. However, the implementation of this measure has fallen short of its potential.

2015 – State (RS) Decree No. 52,431/2015 represents an attempt to no longer oblige the conservation of grassland ecosystems within Legal Reserves, under the allegation that livestock grazing has historically suppressed grassland vegetation, an argument contrary to scientific evidence. However, prior authorisation is required for the suppression of grasslands.

2017 – Decree No. 8,972/2017 establishes the National Policy for Native Vegetation Recovery (PROVEG), which aims to promote policies, programmes and actions for the recovery of degraded areas. In the Brazilian Pampa alone, the goal is to restore 300,000 ha by 2030.

2017 – State (RS) Environmental Council (CONSEMA) resolution No. 360/2017 established guidelines for sustainable livestock production in Legal Reserves and Areas of Permanent Protection on private properties in the Pampa region.

2018 – State (RS) Environmental Council (CONSEMA) resolution No. 372/2018 requires environmental licensing for the conversion of urban and rural grassland vegetation for agricultural or other use.

2020 – State (RS) Law No. 15,434 established the Environmental Code of the Rio Grande do Sul state. This piece of legislation uses similar concepts to the Decree No. 52,431/2015, despite the lack of scientific support. However, prior authorisation is still required for the suppression of grasslands.

17.4 Beyond Area: The Need to Adequately Manage Grasslands and Forest-Grassland Mosaics

Protected areas need to be managed in ways that ensure the achievement of conservation objectives. In the *Campos Sulinos* region, managers often find themselves uncertain about whether human interventions are necessary or allowed, particularly in strictly protected areas. When faced with doubt or uncertainty regarding the outcome of specific types of native vegetation management, the instinct is often to adopt a hands-off approach and allow natural succession to take its course. However, this approach is deleterious to biodiversity conservation of grassland ecosystems. Today, there is a consensus among grassland and savanna ecologists that the very disturbances that hinder succession towards forest communities are essential for the maintenance of grassland and savanna ecosystems and their biodiversity (see Bond 2019 and Andrade et al. 2023, Chap. 8, this volume, for the role of fire and grazing for grassland dynamics and diversity in the *Campos Sulinos*). The perspective on vegetation succession that views disturbances as barriers for successional trajectories is not applicable to disturbance-driven ecosystems such as grasslands (e.g., Bond 2005; see Overbeck et al. 2022 for Brazil's grasslands and savannas). On the contrary, disturbances, such as fire or grazing, are key elements of the dynamics of these systems and necessary for their conservation. Pausas and Bond (2019) trace the prevailing negative perception of fire in conservation debates back to Alexander von Humboldt. During his expedition to South America (1799–1804), Humboldt mistakenly assumed that the open landscapes he encountered in the Llanos savannas, in present-day Venezuela, were the result of deforestation and human-induced degradation. This forest-centred view of nature (Pausas and Bond 2019), held by early conservationists including Humboldt, persists in the conservation debate to this day. One example is misguided initiatives that prioritise tree-planting and forest landscape restoration in open ecosystems (Veldman et al. 2015b). The 'forest bias' in conservation and restoration of grassy ecosystems globally has been acknowledged also for southern Brazil (Pillar and Vélez 2010; Overbeck et al. 2015; see Box 17.2).

Nonetheless, in debates surrounding vegetation management in protected areas, the concept of 'natural succession' often serves as a justification for a management strategy that excludes all human interventions. Succession is often oversimplified, even among ecologists, as a linear process in which a previously disturbed plant community progresses towards a mature community, typically a forest in the textbook perspective. This simplified view of succession as a predictable, linear process with a single outcome has been challenged since the early days of successional theory (Christensen 2014 for a detailed discussion), yet it still pervades the conservation debate in many regions. Within this perspective, the mature forest, which represents the theoretical endpoint of succession or the so-called 'climax community' in regions suitable for forest development, is often considered the only desirable endpoint of succession – and becomes a conservation objective or restoration goal. Consequently, disturbances that impede or divert the successional process

Box 17.2 Forest-Bias and Conservation

Despite a wealth of recent literature pointing out the diversity of grassy ecosystems, their biodiversity and their ecosystem services (Bardgett et al. 2021; Buisson et al. 2022), they still receive less attention in science and conservation than forests. Forests are often considered to be the more important conservation asset, both in the general public and in scientific discourse. Recently, Silveira et al. (2022) drew attention to this problem under the heading of ‘Biome Awareness Disparity’ (BAD). BAD is characterised by the failure to assess the importance of all vegetation types for conservation and restoration policy. Its origins can be traced back to the eigthteenth-century and nineteenth-century European forestry traditions, and it persists today in postcolonial environmental governance beyond Europe due to legacies of colonial environmental policies. These biases have been reinforced by an ecological understanding that overemphasises the role of climate rather than disturbances or management in determining the distribution of vegetation types. An example is the misperception of management practices such as prescribed fire or grazing as equivalent to degradation. Consequently, grassy ecosystems receive less attention, interest, action and knowledge compared with forest ecosystems. This bias has implications for the implementation of conservation and restoration policies in complex landscapes that contain grassy ecosystems. The *Campos Sulinos* region provides examples of BAD, as highlighted by Staude et al. (2023). Their research demonstrates that open ecosystems, including grasslands, harbour more endangered species than forests. However, this is not reflected in current conservation efforts in the region, where grasslands have lost by far more area than forests. This process is not limited to the *Campos Sulinos* region, as grasslands and savannas worldwide have been sacrificed to accommodate the expansion of agricultural frontiers while simultaneously addressing the prevailing bias towards forest conservation and restoration.

from this presumed deterministic endpoint are viewed negatively and should be minimised or excluded whenever possible. Measures like building fences to exclude grazing animals or suppressing wildfires are implemented accordingly. Of course, the conservation of mature forests and their associated biodiversity is a valid objective in forest landscapes, where disturbances are generally perceived as detrimental to biodiversity conservation (e.g., Gibson et al. 2011; Barlow et al. 2016). For forests in the *Campos Sulinos* region, it is well established that disturbances such as fire, grazing or selective logging can reduce biodiversity (Souza et al. 2012), even though it should be noted that disturbances like windthrow, which create gaps in the forest, may play an important role in the regeneration of certain species and thus in the long-term maintenance of the forest ecosystem. This includes *Araucaria angustifolia* (Souza et al. 2012), the prominent species of the *Araucaria* forest that forms mosaics with grasslands across significant portions of the *Campos Sulinos* region.

For grasslands, however, the situation is different. Bond (2019) suggests to discuss grasslands and other open ecosystems in regions where climate allows forest development under the perspective of the Alternative Stable State theory that allows the inclusion of consumer-control (and fire can be considered a consumer; Bond 2005) as a determinant for the presence of different vegetation types. This theory emphasises feedbacks of the system to the environment, considering, for example, fire-vegetation cycles or vegetation-herbivore interactions: disturbances maintain grassy ecosystems, as they impede forest development, while vegetation provides the fuel for burns and the basis of life for grazing animals. This matches our knowledge on forest-grassland dynamics over past millennia (see Behling et al. 2023, Chap. 4, this volume) and currently (see Müller et al., Chap. 16, this volume), emphasising the need to actively use disturbances for grassland conservation. However, despite clear evidence on their positive effects on grassland biodiversity (see Andrade et al. 2023, Chap. 8, this volume), the relevance of grazing and fire for conservation remains poorly recognised outside the academic debate in the *Campos Sulinos* region. In the absence of such disturbances, grassland communities tend to be dominated by few species of tall grasses, which reduce the amount of light and space available for the coexistence of other plant species of the herbaceous stratum. This causes a reduction in local diversity, in addition to an unwanted accumulation of biomass that, under appropriate conditions, can result in catastrophic fire events. Over larger periods, shrub and tree encroachment may lead to the loss of the typical grassland biodiversity (for plants, see Andrade et al. 2023, Chap. 8, this volume; for birds, see Bencke et al. 2023, Chap. 10, this volume). Disturbances, in contrast, generate spatial heterogeneity, shaping the physiognomy of grassland vegetation with different height strata, increasing the supply and diversity of habitats for fauna.

One argument that has been used against the active use of disturbances when managing PAs is that grassland areas on private land already are under livestock grazing (see Box 17.3), sometimes with the use of fire, and that thus the few areas in PAs should be considered as areas were natural processes of forest-grassland expansion could take place, as grasslands are maintained by disturbances elsewhere (Carlucci et al. 2016). While understandable within the context of the past reduction of forests, this argument is problematic for three main reasons. First, given the alarming losses of natural grassland to other land uses (Fig. 17.1) and the lack of implementation of Legal Reserves (see above), this strategy is risky as it is not guaranteed that grasslands on private land will be maintained in sufficient portions. Second, while grazing and fire do maintain grasslands, the actual contribution to conservation depends on the management practices employed. Production-oriented management often differs from conservation-oriented management. Many private grassland areas in the *Campos Sulinos* are degraded by overgrazing (Carvalho and Batello 2009) or invasive species (e.g., Medeiros and Focht 2007; Guido et al. 2016), and their contribution to biodiversity conservation is severely reduced. The same is true for grassland with intensified use that leads to higher productivity at the cost of species richness and resilience to extreme events (e.g., Jaurena et al. 2021). In PAs, management of native vegetation should be conducted in a way that the objective of conservation is met. As good grazing management allows for high productivity and biodiversity conservation (e.g., Nabinger et al. 2000, 2009), the two goals can often be simultaneously achieved. However, in some cases, lower stocking rates or, eventually, the use of fire for conservation purposes could be interesting as well to increase grassland heterogeneity. Third, the low coverage of grassland by PAs (see Table 17.2), together with the high species turnover across regions (see above), means that the existing PAs are important to represent regional grassland biodiversity; if grassland areas within PAs were lost, especially in regions where little grassland remains in private areas around them, parts of grassland biodiversity specific to a region risk being lost. To avoid this, management is necessary. The argument that forest expansion as a natural process should be allowed to happen in protected areas seems interesting at a first glance, as it allows for natural dynamics and leads to vegetation heterogeneity, which is also positive for biodiversity. However, if maintained in any and every situation, in the long term, this strategy will lead to the loss of grasslands that depend on disturbance within PAs, and thus to loss of biodiversity. Any policy of biodiversity conservation whose primary strategy is the exclusion of disturbances is bound to fail in forest-grassland mosaics because it will, by definition, be detrimental to the conservation of those landscapes that depend on disturbances, that is, the grasslands.

Box 17.3 Wilderness Preservation vs. Biodiversity Conservation – Distinct Strategies

Wilderness preservation and biodiversity conservation are two very distinct strategies within the realm of ‘nature conservation’. Wilderness preservation aims to protect nature in its most untouched state, minimising human influence and preserving ‘wilderness’. On the other hand, biodiversity conservation focuses on safeguarding the biological diversity typical of specific regions. These two strategies often clash, particularly in regions like the *Campos Sulinos*, where grasslands rely on active management to thrive under current conditions. Wilderness preservation can lead to biodiversity losses as undisturbed grassland areas may experience species decline or even be lost to forest encroachment. Furthermore, the concept of wilderness preservation may not be practical in a region where human–nature interaction, particularly through the use of grasslands for grazing, has shaped landscapes for centuries. For more detailed information on the distinct goals of wilderness preservation and biodiversity conservation, as well as their implications for land managers, refer to Sarkar (1999).

Active management of grasslands by fire, grazing or mowing for conservation purposes is common practice in many grassland regions of the world (e.g., WallisDeVries et al. 1998; Buisson et al. 2019; Wilcox et al. 2022), including in the North American tallgrass prairie, an ecosystem with many ecological similarities to South Brazilian grasslands (Overbeck et al. 2018). In the North American prairie region, the combination of livestock grazing and fire, known as ‘pyric herbivory’, is considered an effective strategy to maintain open ecosystems by preventing the encroachment of woody species while sustaining rangeland productivity (Wilcox et al. 2022). One key argument for active management is that it increases spatial and temporal heterogeneity, leading to higher species richness not only among plants but also among animals, such as birds (Fuhlendorf and Engle 2001).

The question that remains is which type of management is the most suitable for conservation of grasslands in the *Campos Sulinos* region. As large native grazers are no longer present in the *Campos Sulinos* (with few exceptions, such as the marsh deer, which occurs in very few and very small populations and thus has a minimal impact at the landscape scale), and natural fires are rare under current climatic and landscape conditions, grassland management can be carried out through domestic grazers, prescribed fires or mowing, or combinations. Which process is the most adequate in a specific situation cannot be generalised; this decision will depend both on the specific conservation assets and objectives, the local situation (e.g., size of areas to be managed) and on the socioeconomic context (which includes location within or close to PAs). Grazing with livestock, however, is especially interesting, as it means that conservation can be conducted in partnership with local populations (see also Baggio et al. 2021), which should lead to higher acceptance of conservation: this is especially true for sustainable use PAs but also in strict protection PAs. At any rate, grazing management is likely best implemented in collaboration with land users who have the necessary knowhow (Baggio et al. 2021). Fire can be an effective option where grazing is not possible (e.g., when there are no ranchers with livestock near the PA) or where specific conservation targets are sensitive to grazing (e.g., populations of endangered species that are sensitive to grazing, such as endangered cacti on rock outcrops). Combinations of fire and grazing, as employed in North America, can be interesting; at current, effects of this management strategy are being evaluated in scientific experiments run by researchers from the Universidade Federal do Rio Grande do Sul. Mowing can be an alternative when neither grazing nor fire is possible, such as in PAs within urban settings (e.g., Morro do Osso state park within the city of Porto Alegre; Ferreira et al. 2010). Managers thus have options, and within each of these strategy types, they can define the management regime (e.g., stocking rates or frequency of fire and mowing) that best contributes to the specific local conservation objectives. Importantly, strategies can be combined, with management interventions varying over space and time, to create heterogeneity that is beneficial for landscape biodiversity.

Forest-grassland mosaics contain patches of both ecosystem types, in different proportions. Given the distinct ecology of both types of ecosystems and specifically the distinct role of disturbances, it is clear that conservation management of both must differ: grasslands are maintained through active vegetation management, while in forest, disturbances should be avoided (e.g., by fences or fire breaks). The dynamics at the forest–grassland interface are interesting as they lead to spatiotemporal heterogeneity (see Müller et al. 2023, Chap. 16, this volume). In larger PAs, it may thus be interesting to allow them to happen in specifically designated zones. However, as this will lead to the loss of grassland areas in the long run, it must be carefully balanced with other conservation objectives. Forest–grassland dynamics are a one-way process: development goes from grassland to forest, and not vice-versa. Once a grassland area has been lost, it can take hundreds of years to recover (Veldman et al. 2015a).

17.5 Conclusions

The analyses on the situation of grassland conservation presented here clearly show that efforts to protect grasslands in the *Campos Sulinos* region are insufficient. Under the current rate of land use change, risks of biodiversity losses are real, and may happen fast. The fulfilment of valid environmental legislation, in particular in relation to the RL requirements, is the first step towards a better conservation of South Brazilian grassland: if properly implemented, which would include restoration of degraded areas situated in RL, this would provide for a considerable proportion of grassland preserved in all regions of the *Campos Sulinos*, while also protecting other types of ecosystems. Just as important is an expansion of the Protected Area network in a way that regional biodiversity is conserved in a representative way, which is not the case at the moment. Such actions would constitute an important contribution to the goal to protect 30% of terrestrial areas that are part of the Kunming-Montreal Global Biodiversity Framework. Importantly, grasslands protected in RL and in PAs of the sustainable use category can be under economically interesting use, which means that local farmers can keep managing the grasslands by livestock grazing with economic return. Management strategies, and in particular grazing intensity, need to be compatible with the purpose of biodiversity conservation. However, many studies have shown that biodiversity conservation and productive pasture management are complementary goals that can be achieved by good grazing management (e.g., Nabinger et al. 2009; Boavista et al. 2019; see also Andrade et al. 2023, Chap. 8, this volume). Under such a perspective, grasslands in the *Campos Sulinos* region offer a unique opportunity to conserve biodiversity and the multiple ecosystem services provided by grasslands while at the same time producing high-quality products, principally meat, but also milk, wool and leather. The most efficient way to protect grasslands in the region certainly would be the development of public policy that aims at maintaining grasslands under traditional use as ranching lands. Considering that grasslands provide many important ecosystem services, this could also be supported by the development of payment for ecosystem services schemes.

While we focus, in this chapter, on the conservation of grasslands, we acknowledge that other types of ecosystems in the region continue to need protection and often also are in need of restoration. This is true, in particular, for *Araucaria* forest that has suffered great losses in the past, but also for ecosystems with lesser extent, such as wetlands. When discussing conservation (and restoration) objectives on the landscape scale, the natural distribution of all types of ecosystems in different parts of the *Campos Sulinos* region could offer a guideline. In addition, recent approaches such as the Red List of Ecosystems (Keith et al. 2015) may be helpful as well and their application for the *Campos Sulinos* region should be tested.

In this contribution, we discussed how to maintain healthy grasslands. Clearly, policy change is necessary. Beyond that, we suggest that future discussions should consider treating ways to reach different conservation objectives – be it particular species or specific ecosystem services – in more detail. To do this, many knowledge gaps need to be filled, for example, on population biology of target species for conservation or regarding trade-offs among ecosystem services. Indeed, quantitative data on the provisioning of ecosystem services by grasslands and on the best management strategy to enhance delivery of important ecosystem services, still is very scarce, which impedes more detailed analyses, but also the development of adequate policy. In the light of climate change, of fast land use change, a pattern that likely will not be reverted in the near future, and of still insufficient knowledge for effective restoration of grasslands (Thomas et al. 2023, Chap. 20, this volume), the challenge of conservation of the *Campos Sulinos* will certainly become even bigger in the future. This also means that conservation scientists need, more than ever, focus on the dissemination of research results and of conservation possibilities to society.

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Chapter 18
Río de la Plata Grasslands: How Did Land-Cover and Ecosystem Functioning Change in the Twenty-First Century?

Federico Gallego, Camilo Bagnato, Santiago Baeza, Gonzalo Camba-Sans, and José Paruelo

18.1 Introduction

South Brazilian grasslands are part of a wider ecoregion that extends throughout Uruguay and central western Argentina known as the Río de la Plata Grasslands (RPG) (Soriano et al. 1991). The RPG occupy the large plain formed around the

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estuary of the Río de la Plata, from 28° to 38° South latitude and from 50° to 66.5° West longitude, covering approximately 760.000 km^2. The average annual temperature varies from 13 °C in the South to 20 °C in the North, and average annual rainfall increases from 400 mm.year^{-1} in the Southwest up to 1500 mm.year^{-1} in the Northeast (Oyarzabal et al. 2020). Grasslands, formed by a combination of C3 and C4 grasses and a broad set of herbs, are the dominant vegetation (Perelman et al. 2001; Overbeck et al. 2007; Lezama et al. 2019; Andrade et al. 2019). The RPG has been divided in eight sub-regions based on their geomorphology, soils, drainage and their link with natural vegetation and land-use. These sub-regions are the Rolling Pampa, the Inland Pampa (itself with two divisions, Flat and West), the Austral Pampa, the Flooding Pampa, the Mesopotamic Pampa, the Southern Campos and the Northern Campos (Soriano et al. 1991). The Northern Campos sub-region encompasses the Pampa biome in the south Brazilian grasslands.

In recent decades, the areas occupied by grasslands have been extensively replaced by annual crops, sown pastures and tree plantations (Cordeiro and Hasenack 2009; Graesser et al. 2015; Volante et al. 2015; Baeza and Paruelo 2018, 2020; Souza et al. 2020; Baeza et al. 2022). These land-use and land-cover changes have occurred in a geographical (the RPG) and ecological (temperate and subtropical grasslands) region with very low levels of protection and hence high risks of species biodiversity erosion (Hoekstra et al. 2005; Watson et al. 2016).

Land-use and land-cover changes represent a major alteration of the surface structure (Foley et al. 2005; Ellis et al. 2010; IPBES, 2019). Changes generally involve the replacement of the dominant plant functional types, a mix of C3 and C4 perennial grasses, by perennial trees or annual plants (either dicots or grasses). However, the replacement of grasslands, shrublands and savannas by annual crops and tree plantations not only reduces biodiversity in terms of composition, but it also generates an erosion of the structural and functional diversity (sensu Noss 1990; Fig. 18.1). Such structural and functional dimensions of biodiversity, particularly at the ecosystem and landscape level, are often a neglected aspect of global land-use and land-cover transformations. Alcaraz-Segura et al. (2013) showed the consequences of such changes on the regional climate in the southern part of South America.

Paruelo et al. (2001) and Alcaraz-Segura et al. (2006) introduced the idea of Ecosystem Functional Types (EFT) as an entity able to be used to describe functional diversity at the landscape level using a common protocol and over large areas. EFT were defined as patches of the earth's surface with similar exchange of matter and energy between biota and the physical environment. Alcaraz-Segura et al. (2013) studied the environmental controls of EFT diversity over the whole Río de la Plata basin. As observed for species richness in the southern hemisphere, water availability, not energy, emerged as the main climatic driver of EFT richness in natural areas of temperate South America. In anthropogenic areas, the roles of both water and energy decrease. Richness increases at low levels of human influence, but as human intervention intensifies, biodiversity decreases.

Functional and structural changes would impact on the environmental performance of the landscape (Forman 1995; Wu 2006). Basically, the key question is

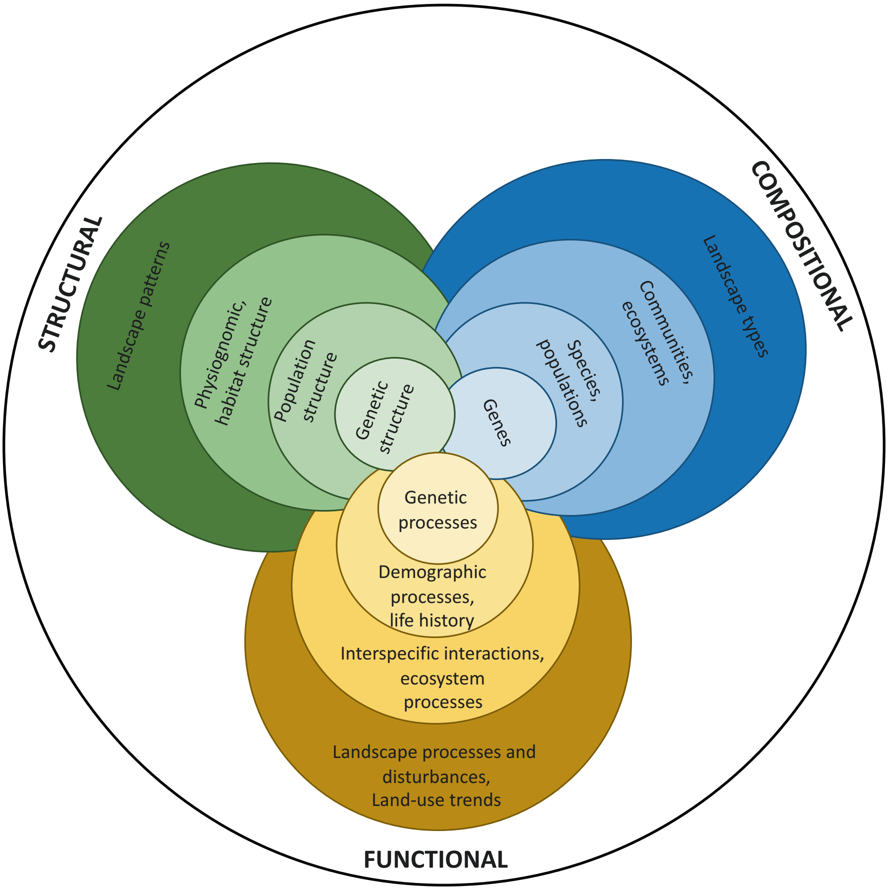

Fig. 18.1 The schematic definition of biodiversity. (Adapted from Noss 1990)

how sustainability changes in time and space (Paruelo and Sierra 2023). An operational definition of sustainability should focus more on the changes than on the absolute value. For example, Wu (2013) defines sustainability as the ability to consistently provide specific Ecosystem Services (ES) for the maintenance and improvement of human well-being over the long term.

Many ecological indicators have been proposed (Burkhard et al. 2012; Paruelo et al. 2016; Englund et al. 2017) to describe ES supply. Such indicators must be sensitive to critical functional changes (i.e. water or C dynamics, energy surface changes), have to be monitored using a common protocol at low cost and should be auditable by third parties. Land-use and land-cover transformation has obvious structural consequences: the replacement and often the homogenization of the landscape. Three indicators may provide a temporal and spatial perspective of the human impact of natural habitat transformation: the diversity of EFT at the landscape level (Alcaraz-Segura et al. 2013), the Ecosystem Service Supply Index (ESSI, Paruelo et al. 2016) and the Human Appropriation of Net Primary Production (Baeza and Paruelo 2018). The first index focuses on changes on functional biodiversity and the last two are based on the effects of human interventions on carbon (C) dynamics. In 2022, the Uruguayan government included these three indicators in the set to describe the environmental footprint of livestock production (Ministerio de Ambiente 2022).

In this chapter, we described the main structural and functional changes that took place in the Río de la Plata Grasslands region in the last two decades focusing on the main land-use and land-cover transitions and the distribution of the EFT. We also analysed some of the consequences derived from land-use and land-cover changes on the diversity of EFT at the landscape level, the supply of ecosystem services and the human appropriation of net primary production. Finally, we speculated on the most likely changes that may occur in the next few years.

18.2 Observed Changes

18.2.1 Structural Changes

The RPG experienced significant landscape transformations over the last two decades (Baldi and Paruelo 2008; Volante et al. 2015; Baeza and Paruelo 2018, 2020). The results of the mapping initiative carried out by the MapBiomas Pampa project (Collection 1; https://pampa.mapbiomas.org/es; Baeza et al. 2022) show that the region had a net loss of native vegetation (woodlands, grasslands and wetlands) of 84,701 km^2 (16.3%) between 2000 and 2019. Particularly, the area occupied by grassland decreased from 36.8% to 29.6% (from 369,647 to 297,795 km^2; a relative change of −19.4%) and the area under cropland and afforestation increased from 42.5% to 49.9% (from 427,239 to 501,489 km^2; a relative change of +17.4%) and 1.4% to 2.3% (from 13,867 to 23,328 km^2; a relative change of +68.2%), respectively (Fig. 18.2). At the country level, Brazil had the greatest proportional loss of grasslands, with 22,967 km^2 (−27.6%), mainly due to the expansion of croplands. Argentina had a grassland loss of 36,571 km^2 (−20.1%), while in Uruguay the reduction was 12,229 km^2 (−11.7%). In the case of Argentina and Uruguay, the reduction of grasslands area was mainly associated with the expansion of croplands and sowed pastures. In the Uruguayan Campos, there was an important increase of tree plantations determining an additional reduction of grasslands area.

All RPG sub-regions, except for the Rolling Pampa (where changes occurred before the analysed period), showed important losses of grasslands between the 2000 and 2019 period. The highest grasslands losses occurred in the Northern Campos and the West Inland Pampa, with a reduction of 27,894 km^2 (a relative change of −18.2%) and 11,261 km^2 (a relative change of −28.2%), respectively. In both cases, losses were associated with the expansion of cropland areas, except for the Northern Campos where afforestation also explained the grassland area reduction. The Flooding Pampa and the Flat Inland Pampa showed the lowest reduction

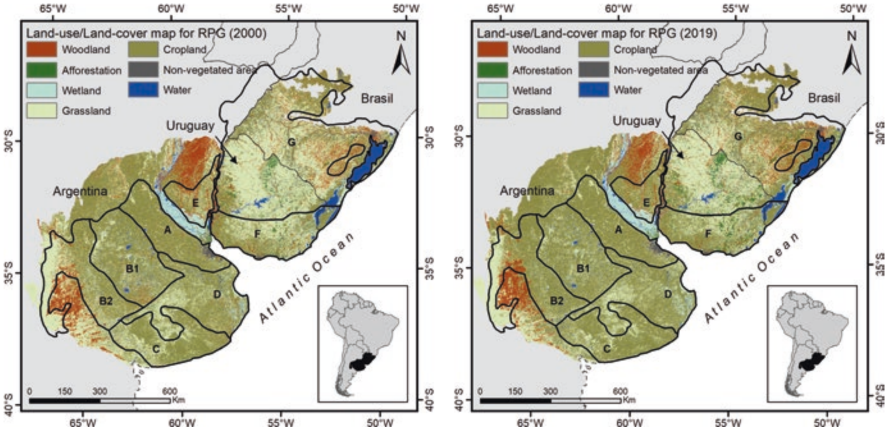

Fig. 18.2 Land-use and land-cover map for the Río de la Plata Grasslands region in 2000 (left) and 2019 (right). Letters denote different sub-regions of Río de la Plata Grasslands: (A) Rolling Pampa. (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Austral Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos. Data from MapBiomas Pampa Initiative Collection1. (https://pampa.mapbiomas.org/es)

in grasslands area, 2086 km^2 (a relative change of −7.8%) and 722 km^2 (a relative change of −4.7%), respectively.

18.2.2 Functional Changes

To characterize and identify changes in the ecosystem functioning associated with land-use and land-cover changes, we mapped the Ecosystem Functional Types (EFT, Paruelo et al. 2001; Alcaraz-Segura et al. 2006). The identification of the EFT was based on the seasonal dynamics of the Normalized Difference Vegetation Index (NDVI). The NDVI is one of the most widely used vegetation indices and shows a positive relationship with the fraction of photosynthetically active radiation absorbed by green vegetation and hence with productivity of the ecosystems (Pettorelli 2013). We used NDVI images from the MODIS sensor (collection 6, Mod13q1). These images have a 250-meter spatial resolution (~6 ha) and 16-day temporal resolution.

EFT were defined through remote sensing techniques and using three ‘phenometrics’ that synthetize the functional behaviour of ecosystems (Alcaraz-Segura et al. 2013): the mean ($NDVI_{MEAN}$), the coefficient of variation ($NDVI_{CV}$) and the date of maximum ($NDVI_{fMAX}$) (see Fig. S18.1 in the Supplementary Material). The range of values of each metric was divided into four intervals, giving a potential number of 64 EFT. In the case of the date of maximum, the intervals corresponded to the four seasons of the year. For the mean and coefficient of variation, we calculated the quartiles of the histograms to define the limits of the four classes. We assigned codes to each EFT as suggested by Paruelo et al. (2001) using two letters and a number (three characters). The first letter of the code (Capital) corresponds to increasing the $NDVI_{MEAN}$ (from 'A' to 'D'). The second letter (lower case) indicates decreasing values of the seasonality ($NDVI_{CV}$) (from 'a' to 'd'). Numbers indicate the season in which the maximum value occurs (1 for spring, 2 for summer, 3 for autumn and 4 for winter). This definition and coding of EFT based solely on descriptors of ecosystem functioning allows for an ecological interpretation of the legend. For example, Aa1 corresponds to an EFT with low radiation interception (productivity), high seasonality and a maximum peak of photosynthetic activity during the spring. The EFT were generated for three periods: 2000, 2010 and 2021. To avoid the effects of specific climatic conditions, the EFT were generated for a four-year average: 2000–2003, 2009–2012 and 2018–2021. To make the three assessed periods comparable, we used the quartiles calculated for 2000–2003 period to build EFT for each period. Thus, we can compare and characterize the shifts among EFT between periods.

The EFT maps provide a synthetic characterization of spatial patterns of ecosystem functioning and their changes between periods in the RPG (Fig. 18.3). The 64 possible combinations of the three functional attributes used to build EFT were identified in RPG. Table 18.1 provides an interpretation of the most abundant EFTs for RPG that together account for almost 70% of the total area. Despite the period considered, the most abundant EFT was Aa2, a low radiation interception, high seasonality and a summer peak ecosystem. This EFT characterizes agricultural areas mainly in the Rolling and Inland Pampa. The EFT mainly linked to grassland ecosystems were Dd2, Cd1 and Cd3 (Fig. 18.3 and Table 18.1). In all cases, these EFT were mainly located in the Southern and Northern Campos and were characterized by a high radiation interception, low seasonality and a spring/summer/autumn peak ecosystem.

The highest values of $NDVI_{MEAN}$ were found in Northern Campos generally associated with afforestation and some woodlands relicts (Fig. S18.1 in the Supplementary material). The lowest values of $NDVI_{MEAN}$ presented an even distribution among the whole study area associated with bare soil due to seasonal water bodies and dunes next to the coastlines. High seasonality ecosystems were related to agricultural foci mainly in the West, Inland and Rolling Pampa in Argentina and in the very north of Northern Campos in Brazil. Flooding Pampa and most of Uruguayan natural grassland (Southern and Northern Campos sub-regions) presented the lowest seasonality, including the lands converted to evergreen tree plantations. Most of the EFTs identified showed an $NDVI_{fMAX}$ in summer covering 388,000 km^2 in 2000–2003, 496,00 km^2 in 2009–2012 and 312,000 km^2 in 2018–2021. The phenological indicator of growing season $NDVI_{fMAX}$ showed that most ecosystems of RPG have a summer peak. This is particularly clear in the most transformed areas where conversion to agriculture determines high seasonality as well. Nevertheless, autumn and spring peaks ecosystems can be found across large areas of central RPG, mostly in Uruguay and Flooding and Austral Pampa in Argentina. Areas with winter peak are rare but can be found in specific spots located in the Northern Campos and Mesopotamic Pampa (see Fig. S18.1 in the Supplementary material).

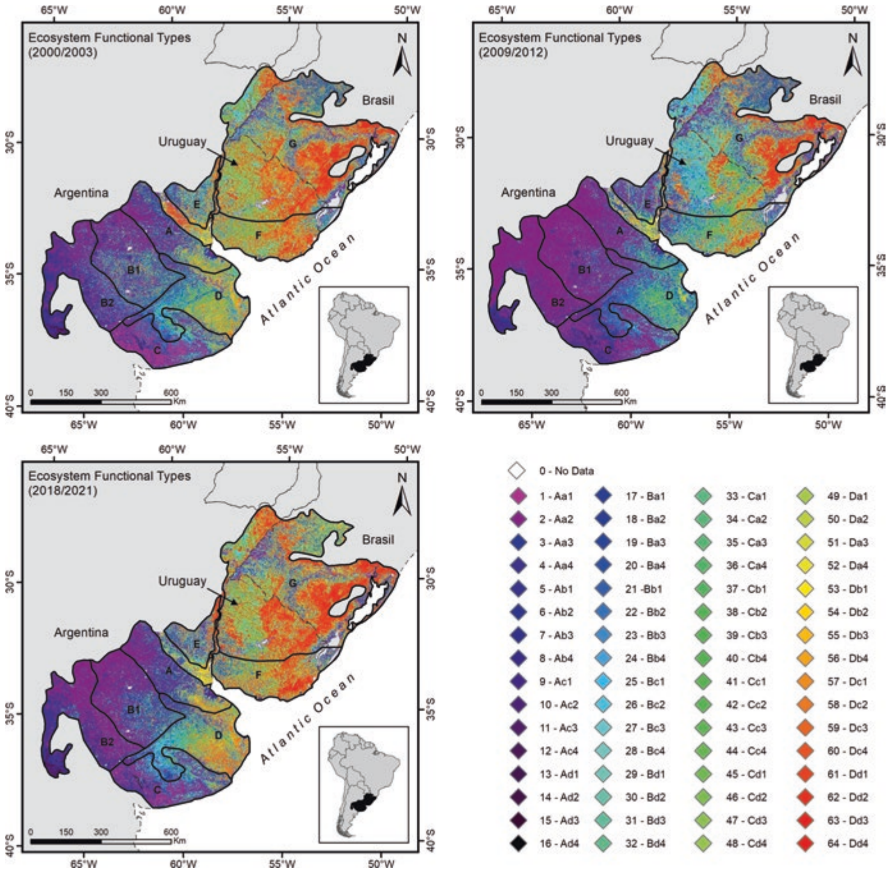

Fig. 18.3 Ecosystem Functional Types for the Río de la Plata Grasslands region in the three study periods (2000–2003, 2009–2012 and 2018–2021). Letters denote different sub-regions of Río de la Plata Grasslands: (A) Rolling Pampa. (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Austral Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos

18.3 Consequences of the Structural and Functional Changes

18.3.1 Functional Diversity at the Landscape Level

Functional diversity was assessed for each analysed period using the Shannon-Wiener Diversity Index (Fig. 18.4). We defined a 10 × 10 km grid and we calculated the diversity of EFTs for each cell using the 'landscapemetrics' R package (Hesselbarth et al. 2019). Changes in functional diversity were calculated as the percentage of change between 2000–2003 and 2018–2021 periods (Fig. 18.4).

Table 18.1 Description of most abundant Ecosystem Functional Types (EFT) in the Río de la Plata Grassland region for the 2018–2021 period

EFT	Area [Mha]	EFT interpretation	Geographic distribution and land-use and land-cover correspondence
Aa2	13.82	Low radiation interception, high seasonality and summer peak	Mostly agriculture in Rolling and Inland Pampa
Ba2	7.20	Lower intermediate radiation interception, high seasonality and summer peak	Agriculture distributed in all RPG
Dd1	5.32	High radiation interception, low seasonality and spring peak	Mostly natural vegetation (woodlands), but also include afforestation in Southern and Northern Campos
Dd3	4.19	High radiation interception, low seasonality and autumn peak	
Dd2	4.11	High radiation interception, low seasonality and summer peak	
Bb2	3.34	Lower intermediate radiation interception, upper intermediate seasonality and summer peak	Transformed ecosystems evenly distributed in all RPG
Ab2	2.73	Low radiation interception, upper intermediate seasonality, and summer peak	Semi-natural grasslands ecosystems located in the West Inland Pampa. Small patches of herbaceous vegetation distributed in Argentinian portion of RPG
Dc1	2.45	High radiation interception, low seasonality and spring peak	Semi-natural wetlands in Flooding and Rolling Pampa and riparian forest in Mesopotamic, Southern and Northern Campos
Cd1	2.26	Upper intermediate radiation interception, low seasonality and spring peak	Mainly natural grasslands in Uruguay and Brazil
Cb2	2.24	Upper intermediate radiation interception, upper intermediate seasonality and summer peak	Small patches distributed in all regions of RPG mainly associated with natural vegetation as dry seasonal forest, wetland vegetation and some transformed areas
Ca2	2.21	Upper intermediate radiation interception, high seasonality and summer peak	Mainly agricultural ecosystems in Northern Campos
Cd3	2.16	Upper intermediate radiation interception, low seasonality and autumn peak	Grassland ecosystems in Southern and Northern Campos
Cc2	2.04	Upper intermediate radiation interception, lower intermediate seasonality and summer peak	Small patches of transformed and semi-natural vegetation distributed in central and northern RPG

(continued)

Table 18.1 (continued)

EFT	Area [Mha]	EFT interpretation	Geographic distribution and land-use and land-cover correspondence
Cc1	2.03	Upper intermediate radiation interception, lower intermediate seasonality and spring peak	Herbaceous vegetation mainly in Flooding Pampa and Southern Campos
Dc2	1.90	High radiation interception, lower intermediate seasonality and summer peak	Riparian forest and humid herbaceous vegetation mainly in Northern Campos

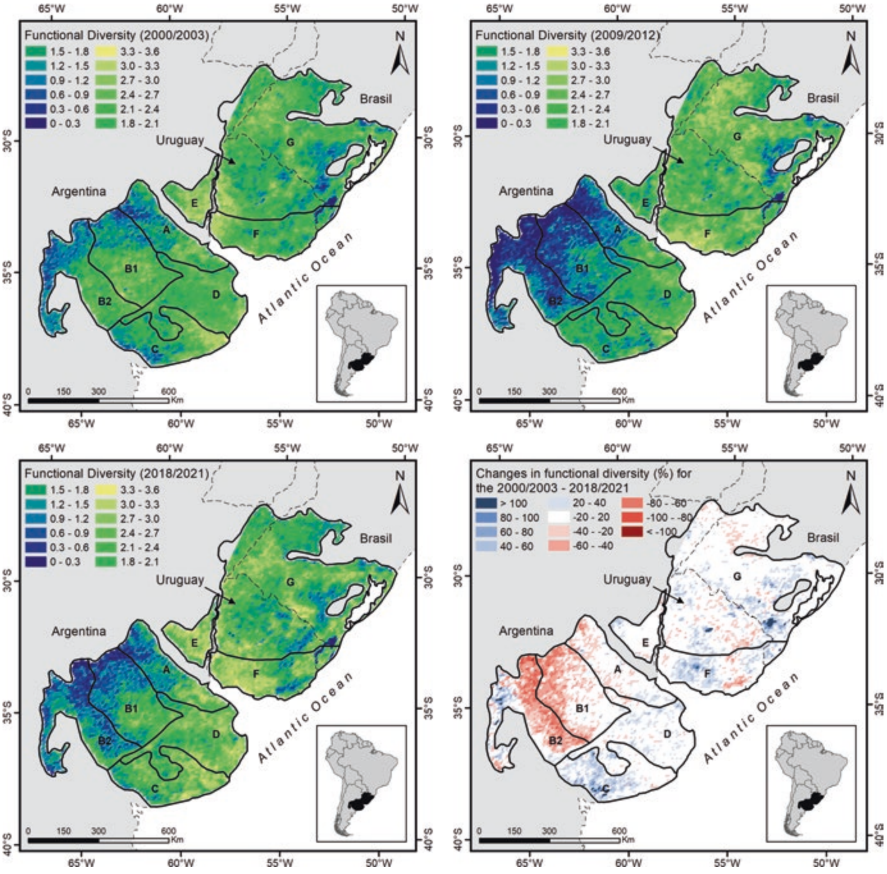

Fig. 18.4 Functional Diversity for the Río de la Plata Grasslands region represented by the Shannon-Wiener Diversity Index in the three study periods (2000–2003, 2009–2012 and 2018–2021); and changes in functional diversity expressed as the percentage of change in the Shannon-Wiener Diversity Index between 2000–2003 and 2018–2021 periods. Letters denotes different sub-regions of Río de la Plata Grasslands: (A) Rolling Pampa. (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Austral Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos

EFT diversity showed a heterogeneous pattern with low functional diversity values in the south-west driest portion of RPG and high diversity zones interspersed across all the sub-regions. The maximum values of functional diversity were found in transitional sub-regions characterized for having both natural vegetation relicts and transformed areas such as the Flooding Pampa and Southern Campos. The lower diversity areas seem to be associated with very transformed and homogenized agricultural areas of the Inland and Rolling Pampa. Indeed, the functional diversity diminished greatly in the Rolling and Inland Pampa during the last 20 years. In the Southern and Northern Campos, functional diversity generally increased. Flooding and Austral Pampa in Argentina showed greater values of Shannon-Wiener Diversity Index in 2018–2021 than in the 2000–2003 period.

18.3.2 Ecosystem Service Supply

Paruelo et al. (2016) presented a synoptic indicator of 'bundles' supporting and regulating ES related to C dynamics, the 'Ecosystem Services Supply Index' (ESSI). It is based on vegetation indices derived from remote sensing data, which constitute robust estimators of Net Primary Productivity (NPP) (Monteith 1972; Piñeiro et al. 2006), an integrating variable of ecosystem functioning (McNaughton et al. 1989). The ESSI merges two attributes of the NDVI annual dynamics: the annual average ($NDVI_{MEAN}$, a proxy of total C gains) and the intra-annual coefficient of variation ($NDVI_{CV}$, an indicator of seasonality): $ESSI = NDVI_{MEAN} * (1 - NDVI_{CV})$. Those sites where annual productivity is higher and more seasonally stable would have a higher ES supply.

The foundation of the ESSI is based on both the conceptual framework of the ES cascade model and the ES bundles concept (Raudsepp-Hearne et al. 2010). According to this scheme, the ESSI represents an integrative index of ecosystem functioning which gives rise to the cascade. It can describe the variation in different regulating and supporting ES (some of them intermediate and others final ES) that vary together in the same direction (ES bundles). The support for using ESSI as a proxy of ES supply was originally based on its positive relationship with four ES estimated from empirical data or mechanistic models: groundwater recharge and avian richness in Dry Chaco forests and soil organic carbon (SOC) in the RPG (Paruelo et al. 2016). Two additional studies provided additional support to the use of ESSI (Weyland et al. 2019; Staiano et al. 2021). The index has been used in a variety of systems to evaluate spatial and temporal patterns of the environmental footprint of agricultural activities (Verón et al. 2018; Staiano et al. 2021; Gallego et al. 2020; Jullian et al. 2021; Camba-Sans et al. 2021).

The ESSI showed a clear regional pattern (Fig. 18.5). The heterogeneity in mean ESSI (2000–2021) is associated with both environmental gradients and land-cover transformation. ESSI values showed a NE-SW gradient clearly associated with the precipitation and temperature gradient, the major controls of C gains and its seasonality (Paruelo and Lauenroth, 1998; Guerschman et al. 2003). However, it is

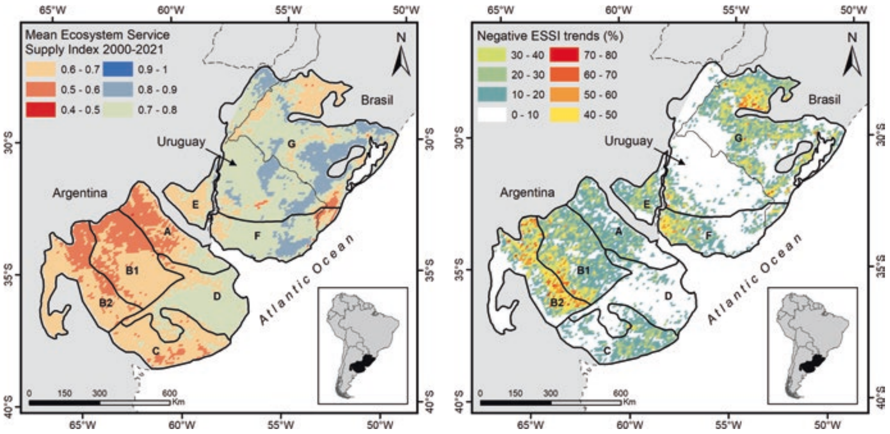

Fig. 18.5 Left: Mean Ecosystem Service Supply Index value (2000–2021), and right: percentage of negative significant trends (over a 10 × 10 km grid) in the Ecosystem Service Supply Index over the period 2001–2021 for the Río de la Plata Grasslands. Letters denote different sub-regions of Río de la Plata Grasslands: (A) Rolling Pampa. (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Austral Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos

possible to identify areas with low ESSI values associated with agricultural foci (see Fig. 18.2; MapBiomas Pampa Collection 1, 2021). Paruelo et al. (2022) analysed the ESSI of the natural habitats of the RPG. They found that ES supply in grasslands, shrublands and savannas was higher than the values of transformed land-cover (approx. a 15% higher). The exceptions are tree plantations which present the highest values.

In addition to the mean ESSI values, the temporal trends provide a more informative context involving temporal dynamics. Therefore, we analysed the temporal trend of the ESSI for the 2000–2021 period using the Mann-Kendall test. The results are presented in a grid with a resolution of 10 × 10 km (Fig. 18.5). Positive trends occupied 11% of the RPG and were observed almost exclusively on afforested areas. On the other hand, negative trends covered 14% of the study area and were associated with cropland areas. Non-significant trends occupied the largest proportion (75%) of the RPG and were mostly associated with natural ecosystems. Again, clear regional patterns emerge. However, in this case, the observed differences are more strongly associated with the land-use and land-cover patterns than with environmental factors. Over the past two decades, approximately 25% of the non-grassland area (mainly croplands) of the Río de la Plata Grasslands region experienced a reduction in the supply of ecosystem services. Additionally, less than 4% of the grassland area showed a significant decrease in ecosystem service supply between 2001 and 2021.

18.3.3 Human Appropriation of Net Primary Production

The Human Appropriation of Net Primary Production (HANPP) quantifies the portion of ecosystems NPP used directly or indirectly by humans (Vitousek et al. 1986), and it reflects the changes in available energy for the trophic web (Field 2001). HANPP incorporates two aspects of agricultural intensification described above: increases in cultivated area and increases in crop yield. Several works have shown the relationship between HANPP and biodiversity (Wright 1990; Haberl 1997; Haberl et al. 2004), changes in atmospheric composition (DeFries et al. 1999; Schimel 2000), water cycles (Gerten et al. 2005) or the provision of ecosystem services (Daily 1997; Millennium Ecosystem Assessment 2005). The central role of energy flow and its linkage with other ecosystem processes make HANPP a comprehensive indicator of human impact on ecosystems.

Haberl (1997) defined HANPP as the sum of the harvested Net Primary Production (NPP) and the differences in NPP due to land-use changes. HANPP results from the difference between the NPP in the absence of human influence (NPP of potential vegetation: NPP_0) and the NPP of the actual vegetation remaining after harvest ($\mathrm{NPP}_{\mathrm{REM}}$). $\mathrm{NPP}_{\mathrm{REM}}$ was calculated as the NPP of the current vegetation ($\mathrm{NPP}_{\mathrm{ACT}}$) minus the harvested NPP ($\mathrm{NPP}_{\mathrm{H}}$), directly appropriated by humans as agricultural products (grain, wood, meat, etc.) or destroyed during harvest (Fig. 18.6, Eq. 18.1).

$$\mathrm{HANPP} = NPP_0 - NPP_{REM} = NPP_0 - \left(NPP_{\mathrm{ACT}} - NPP_{\mathrm{H}}\right) \tag{18.1}$$

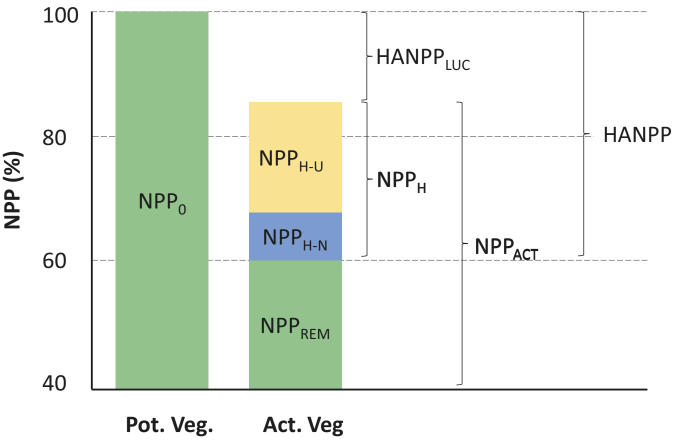

Fig. 18.6 Components involved in Human Appropriation of Net Primary Productivity (HANPP) calculation. NPP_0: NPP of potential vegetation (Pot Veg); $\mathrm{NPP}_{\mathrm{ACT}}$: NPP of the current vegetation; $\mathrm{NPP}_{\mathrm{REM}}$: NPP of current vegetation remaining after harvest; $\mathrm{NPP}_{\mathrm{H}}$: harvested NPP; $\mathrm{NPP}_{\mathrm{H-U}}$: harvested NPP used by humans as agricultural products (grain, wood, meat, etc.); $\mathrm{NPP}_{\mathrm{H-N}}$: harvested NPP not used (crop residues, underground biomass); $\mathrm{HANPP}_{\mathrm{LUC}}$: HANPP due to land-use changes

The difference between NPP_0 and NPP_{ACT} represents HANPP due to land-use changes ($HANPP_{LUC}$), so HANPP can also be formulated as (Eq. 18.2):

$$\mathrm{HANPP} = NPP_{\mathrm{H}} + \mathrm{HANPP}_{LUC} \tag{18.2}$$

Baeza and Paruelo (2018) used medium resolution land-use and land-cover maps and NPP estimates from sub-national level agricultural statistics, and remotely sensed data modelling to calculate the HANPP for the entire Río de la Plata Grasslands in two periods that encompass a strong agricultural intensification process, 2001–2002 and 2012–2013. They found that more than 40% of RPG region NPP is appropriated every year (and used directly or indirectly) by humans, a percentage much higher than that found in other regions of the world (see, e.g. Vitousek et al. 1986; Rojstaczer et al. 2001; Haberl et al. 2007). HANPP increased from 42% of potential NPP on 2001–2001 to 46.5% on 2012–2013 due to the strong process of agricultural intensification that took place in the RPG region. HANPP was highest in agricultural and forestry foci where it may exceed 70–80%, and it was mainly associated with increases in harvested NPP due to both the expansion of the cultivated area and the crop yields (Fig. 18.7).

Maximum HANPP average values for the different RPG sub-regions occurred in the Rolling Pampa, reaching 8.338 and 8.291 kgDM ha^{-1} $year^{-1}$ for 2001–2002 and 2012–2013, respectively. Minimum average values occurred in Southern Campos during 2001–2002 (4.070 kgDM ha^{-1} $year^{-1}$) and in Flooding Pampa during 2012–2013 (4.199 kgDM ha^{-1} $year^{-1}$). The largest increases occurred on both sides of the Uruguay River (Mesopotamic Pampa, West of Southern Campos and southwest of Northern Campos), the North-western half of the Rolling Pampa, east of the

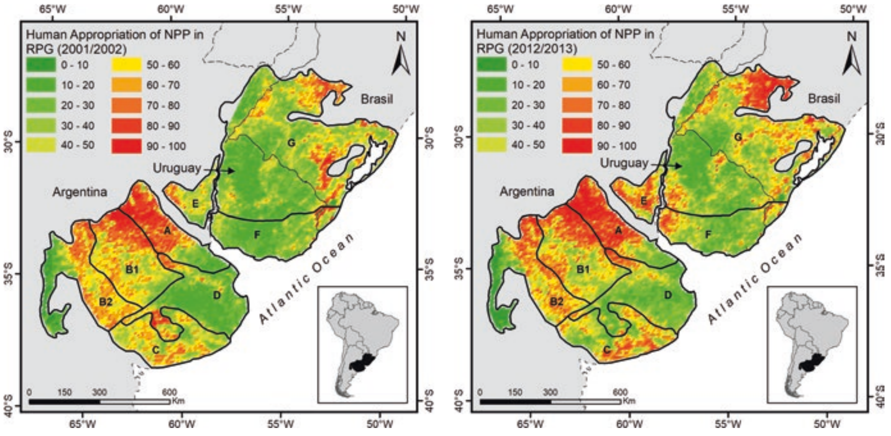

Fig. 18.7 Human Appropriation of Net Primary Productivity (HANPP) in the Río de la Plata Grasslands region, expressed as a percentage of Net Primary Productivity of potential vegetation for 2001–2002 and 2012–2013. Letters denotes different sub-regions of Río de la Plata Grasslands: (A) Rolling Pampa. (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Austral Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos

Southern Pampa, north of the Northern Campos, some sectors of the Inland Pampa (Flat and West) and northwest of the Northern Campos (the Brazilian side of the Argentina–Brazil border) (Fig. 18.7).

18.4 Expected Land-Use and Land-Cover Changes

Using the MapBiomas Pampa land-use and land-cover maps, we described the transition probabilities $p_{i\text{->}j}$ between land-use and land-cover types considering two study periods (2000–2010 and 2010–2019, Fig. 18.8). This allows us to estimate the

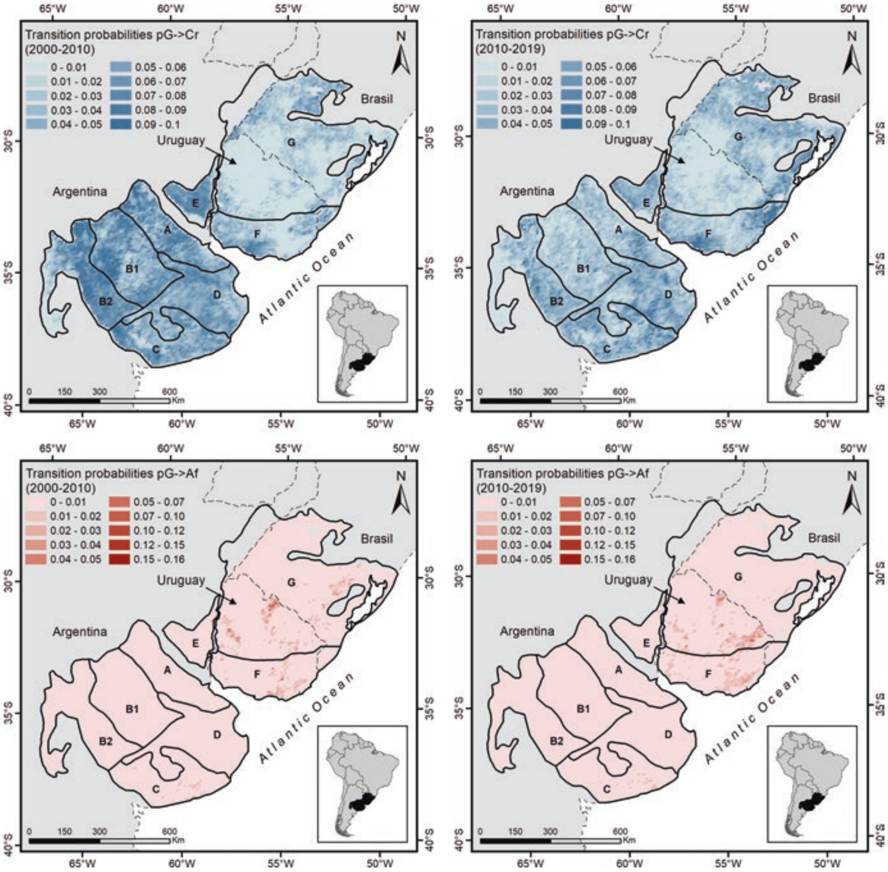

Fig. 18.8 Transition probabilities for grassland to cropland ($p_{G\text{->}Cr}$, blue) and grassland to afforestation ($p_{G\text{->}Af}$, orange) in the RPG for 2000–2010 and 2010–2019. Letters denote different subregions of the RPG: (A) Rolling Pampa. (B1) Flat Inland Pampa, (B2) West Inland Pampa, (C) Austral Pampa, (D) Flooding Pampa, (E) Mesopotamic Pampa, (F) Southern Campos, (G) Northern Campos

annual rates of change and at which land-use and land-cover types expense the changes occurred. We overlapped the two period's maps to obtain the transitions between land-use and land-cover types. We analysed the main transformations that occurred in the RPG over the last decades: (a) grassland to cropland (G->Cr) and (b) grassland to afforestation (G->Af) (Baldi and Paruelo 2008; Baeza and Paruelo 2018; Baeza et al. 2022). We then intersected these transition maps with a 10 × 10 km grid to calculate the transition probabilities as (Eq. 18.3):

$$P_{i \to j,k} = \frac{A_{i \to j,k}}{A_{i,t=0,k}} \times \frac{1}{\Delta t} \tag{18.3}$$

where A_i is the initial (at $t = 0$) area occupied by land-use and land-cover types i, $A_{i\text{->}j}$ the area of transition class i->j during Δt (the time period in years) and k a grid cell.

On average, for the whole region, transition probabilities from grassland to cropland were 0.047 and 0.033 for the 2000–2010 and 2010–2019 periods, respectively. The transition probabilities from grassland to afforestation were 0.001 and 0.0012, for the 2000–2010 and 2010–2019 periods, respectively.

At RPG sub-regions level, the transition probabilities were different according to the land-use and land-cover types and the period of study. For the 2000–2010 period, the Argentine Pampa showed the highest annual probability of changing to cropland (average $p_{G\text{->}Cr} = 0.055$), particularly, the Mesopotamic Pampa, Rolling Pampa and West and Flat Inland Pampa (Table 18.2). On the other hand, for the 2010–2019 period, only the Austral Pampa, the Mesopotamic Pampa and the Flooding Pampa showed high probabilities of change (Table 18.2). The rest of the sub-regions showed low transition probabilities (average $p_{G\text{->}Cr} = 0.024$).

Grassland showed the highest annual probability of changing to afforestation in the Southern Campos and Northern Campos for both the 2000–2010 and 2010–2019 periods (Table 18.2). The rest of the sub-regions showed very low values for both periods (average 2000–2010, $p_{G\text{->}Af} = 0.0003$; average 2010–2019, $p_{G\text{->}Cr} = 0.0004$).

Table 18.2 Transition probabilities from grassland to afforestation ($p_{G\text{->}Af}$) and grassland to cropland ($p_{G\text{->}Cr}$) for each RPG sub-region and for the two periods under study (2000–2010 and 2010–2019)

	2000–2010		2010–2019	
Sub-region	$p_{G\text{->}Af}$	$p_{G\text{->}Cr}$	$p_{G\text{->}Af}$	$p_{G\text{->}Cr}$
Northern Campos	0,00234	0,01626	0,00209	0,02416
Southern Campos	0,00340	0,02740	0,00535	0,03639
Austral Pampa	0,00122	0,05023	0,00138	0,04187
West Inland Pampa	0,00001	0,05692	0,00007	0,03045
Flat Inland Pampa	0,00010	0,05632	0,00014	0,02408
Flooding Pampa	0,00003	0,04860	0,00006	0,03827
Mesopotamic Pampa	0,00058	0,06118	0,00061	0,04078
Rolling Pampa	0,00007	0,05684	0,00006	0,03111

Considering the observed trends in relation to the transition probability, an increase in afforestation area is expected, particularly in the Northern and Southern Campos, and a neutral or even retracting trend in the transition from grassland to croplands, particularly in the Argentinean Pampa regions where most of natural grasslands have been transformed already.

18.5 Final Considerations

More than 50% of the RPGs have already been transformed. Natural habitats and grasslands were reduced to small relicts in many of the sub-regions (i.e. the Rolling Pampa). The Northern and Southern Campos in Uruguay and Brazil concentrate most of the remaining temperate grasslands in South America. The probability of an area of grassland being replaced by annual crops is more than twice as high as that of being replaced by tree plantations. Both the area covered by grasslands and the probability of being replaced differed markedly among sub-regions indicating that aside from environmental controls, land-use and land-cover distribution is strongly influenced by social, economic and technological factors, which in turn are affected by national policies.

The functional diversity at the landscape level, the Ecosystem Service Supply Index and the Human Appropriation of Net Primary Productivity clearly and objectively showed the consequences of the replacement of grassland by cropland and afforestation. The replacement of grasslands with croplands generates a homogenization of Ecosystem Functioning and a loss of functional diversity. The supply of ES sharply decreased in those areas transformed into croplands. The absence of temporal trends in ES supply was associated with the preservation of natural habitats. Finally, Human Appropriation of Net Primary Productivity increased 4.5% over the entire region between 2001–2002 and 2012–2013. Appropriation surpassed the 70–80% of the Net Primary Productivity of potential vegetation (NPP_0) in agricultural and afforested areas. On average, the HANPP on the grasslands areas is less than 11%; values substantially lower than the regional average (42%).

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Chapter 19
Invasive Alien Species in the *Campos Sulinos*: Current Status and Future Trends

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19.1 General Background of Biological Invasions

In previous centuries, species introductions into new regions were widely celebrated by societies, as they were "enriching" the flora and fauna mainly to improve domestic stock and supply additional food (Simberloff and Rejmánek 2011). Through this process, humans connected regions that were naturally separated by *geographical barriers* and began to alter the limits of species distributions. As contemporary

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anthropic actions have escalated, the extent and frequency of species transfer around the world have been increasing, expanding the distributional range of organisms at accelerated rates (Mack et al. 2000; Seebens et al. 2017). As a result, we often observe species outside of their *native range* coexisting with local biodiversity. However, some species introductions were also unintentional, and many concerns related to changes in natural species distributions came out in the last century. Researchers have tried to gain an insight into processes and consequences of biological invasions across environments by assessing: (i) which species invade; (ii) which habitats are invaded; (iii) what are the impacts of invasions, and (iv) how we can manage them. In this chapter, we aim to answer these questions by focusing on the *Campos Sulinos* region. We (1) briefly provide background on the topic of biological invasions, by introducing the main concepts, the idea of invasion stages, and the classical hypothesis involved; (2) show invasion patterns, highlighting the invaded areas and the most important invasive alien species (IAS) in the *Campos Sulinos*; (3) present the main drivers and impacts of invasion, and (4) introduce the challenging management strategies. Finally, (5) we come up with a brief reflection about the future of the invasions in the ongoing global change scenario and some recommendations to keep moving forward in IAS management.

The invasion process begins with the *transport* of a species from its historical biogeographic distribution (i.e., *native range*) to a new ecosystem, carried on a human-assisted *vector* along a *route* (i.e., *invasion pathway*). This transport could be intentional, when there is a specific intentional purpose (e.g., cultivated plants or domestic animals), or unintentional, as the by-product of the movement of other goods (e.g., contaminated crops seeds or ballast water). The organisms, which survived the transport, are *introduced* to a region beyond their native range (i.e., *alien species*), can *establish* in the wild by forming viable self-standing populations (i.e., *naturalized species*), and may *spread* substantially from their point of introduction, becoming *invasive alien species* (Fig. 19.1; Box 19.1; Richardson et al. 2000; Richardson and Pyšek 2006; Blackburn et al. 2011).

The invasion process can be divided into sequential stages (i.e., transport, introduction, establishment, and spread) which differ in the nature of the barriers imposed (i.e., geography, captivity or cultivation, survival, reproduction, and dispersal), and therefore the mechanisms required to overcome them (Fig. 19.1; Richardson and Pyšek 2006; Blackburn et al. 2011). According to the *Tens rule hypothesis* (see Box 19.2), approximately 10% of the introduced species successfully take consecutive steps of the invasion process (Williamson and Brown 1986; Williamson and Fitter 1996). Thus, not all alien species will survive and reproduce in a new ecosystem, and not all naturalized species are capable of dispersing large areas and becoming invasive. Which alien species are potential invaders and which ecosystems are more invasible have been the main challenging questions in biological invasion research (Rejmánek 1995).

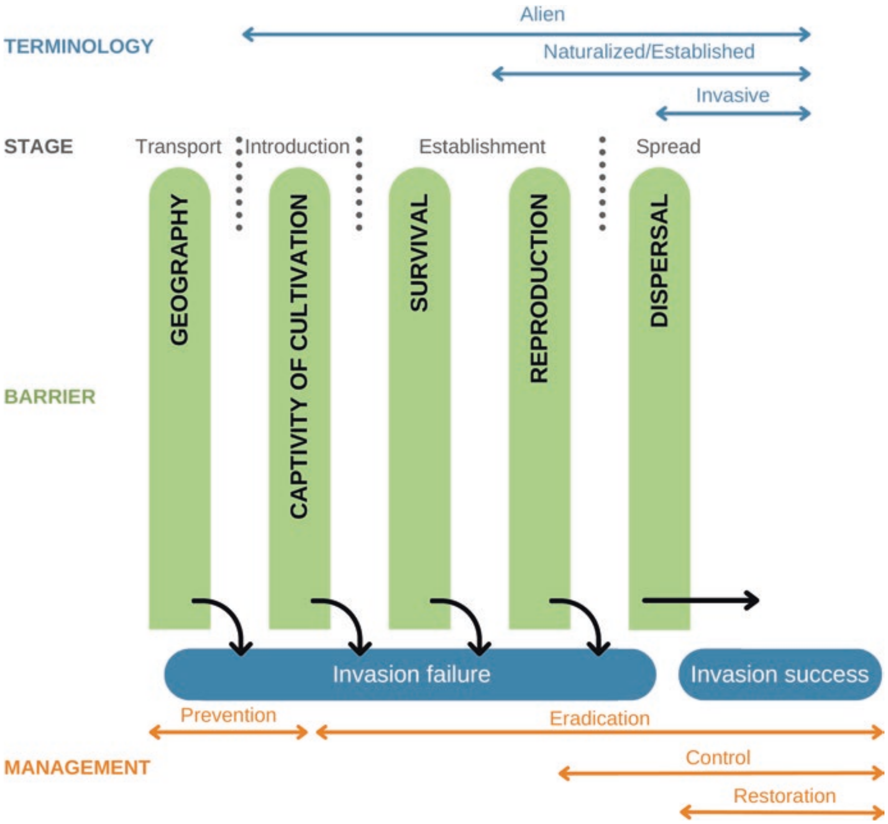


Fig. 19.1 Framework of biological invasions, with indication of barriers and management actions according to the stage of the invasion process and definition of terms used for alien species. (Modified from Richardson et al. 2000 and Blackburn et al. 2011)

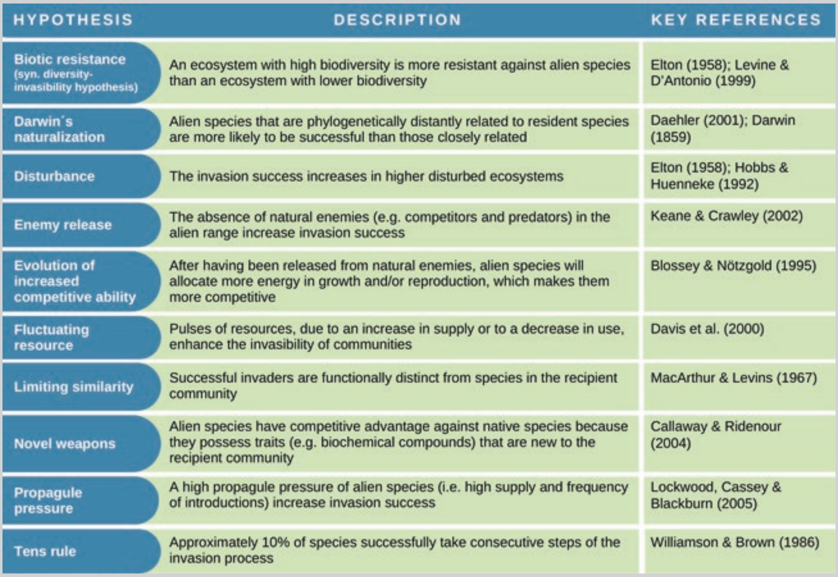
According to the National Invasive Alien Species Database (http://bd.institutohorus.org.br) for Brazil, created and managed by the Horus Institute for Environmental Conservation and Development, there are 481 invasive alien species (IAS) in Brazil, of which 267 (55.5%) are animals, 209 (43.5%) are plants, and five species belong to other Kingdoms. Studies that have analyzed this database found the south and the southeastern of Brazil are most invaded regions (Dechoum et al. 2021). Particularly in the *Campos Sulinos*, the attention regarding alien species occurrence has been increasing in the last years. For instance, the three southern states (Rio Grande do Sul, Santa Catarina, and Paraná) have taken a great step with the publication of official lists of IAS. The first state to publish such a list was Paraná in 2007, which has been updated twice, and in 2015 included 71 species of plants and 140 of animals (Portaria IAP 59/2015). The official list of Santa Catarina

Box 19.1:
Glossary with key concepts used in research on biological invasion, or ecological concepts adapted for the context of biological invasion

CONCEPT	DEFINITION	REFERENCES
Alien range (syn. non-native, exotic, or introduced range)	The distribution area to which a species was transported due to human actions, and did not naturally occur before	[2]
Alien species (syn. non-native, exotic, introduced species)	Those whose presence in a region is due to human actions that enabled them to overcome biogeographical barriers	[2]
Biological invasions (syn. bioinvasions, biotic invasions, species invasions)	The processes involved in determining: (i) the transport of organisms through human activity to areas outside their native range and (ii) the fate of such organisms in their new ranges (survival, establishment, reproduction, dispersion, spread, impact)	[2]
Biotic resistance	The ability of resident species to limit the establishment, survival and/or spread of alien species	[2]
Control	A management action that aims the suppression of an invasive alien species within a defined geographic area	[3]
Eradication	A management action that aims the extirpation of the entire population of an invasive alien species within a designated management unit	[2;3]
Establishment	Stage of the invasion process whereby an alien species forms self-sustaining populations over multiple generations without (or despite) human intervention	[3]
Impact	The environmental and/or socioeconomic changes that invasive species cause in the recipient ecosystems	[2]
Introduction	Stage of the invasion process regarding the movement of a species, intentionally or unintentionally, due to human activity, from an area where it is native to a region outside that range	[2]
Invasibility	The properties of a community, habitat or ecosystem that determine its inherent vulnerability to invasion	[2]
Invasive species	Alien species that sustain self-replacing populations over several life cycles, produce reproductive offspring, often in large numbers at considerable distances from the parent and/or site of introduction, and have the potential to spread over long distances	[2]
Invasiveness	The features of an alien species (e.g. life-history traits) that define its capacity to invade (i.e. to overcome the barriers of the invasion process)	[2]
Management	Activities undertaken to prevent, eradicate or control invasive alien species	[3]
Native range	The distribution area to which a species occurrence is due to its evolution history and natural dispersal	[1]
Native species (syn. indigenous species)	Species whose presence in a region is due to its evolution history and natural dispersal	[2]
Naturalized species (syn. established)	Alien species that sustain self-replacing populations for several life cycles or a given period of time (10 years is advocated for plants) without (or dispite) the direct intervention of humans	[2]
Pathway	A combination of processes and opportunities that result in the human-mediated movement of alien taxa from one area to another	[2;3]
Propagule pressure (syn. introduction effort)	Composite measure consisting of the number of individuals released in a region, resulting from the number of individuals introduced in an introduction event (i.e. propagule size) and the frequency of introduction events (i.e. propagule number)	[4]
Spread (syn. expansion)	The process whereby a naturalized species expands into new areas (usually new regions, rather than local-scale movements) owing to natural or human-mediated dispersal	[2]
Vector	A broadly defined phenomenon involving dispersal mechanisms that can be both non-human mediated (wind, water, birds, mammals, amphibians, etc.) and human mediated	[2]

[1] Blackburn et al. (2011) A proposed unified framework for biological invasions. Trends in ecology & evolution, 26(7), 333-339. [2] Richardson et al. (2011) A compendium of essential concepts and terminology in invasion ecology. Fifty years of invasion ecology: the legacy of Charles Elton, 1, 409-420. [3] Simberloff & Rejmánek (2011) Encyclopedia of Biological Invasions, 1st ed. University of California Press [4] Lockwood et al. (2005) The role of propagule pressure in explaining species invasions. Trends in ecology & evolution, 20(5), 223-228.

Box 19.2:
Principal hypotheses used to explain biological invasions



HYPOTHESIS	DESCRIPTION	KEY REFERENCES
Biotic resistance (syn. diversity-invasibility hypothesis)	An ecosystem with high biodiversity is more resistant against alien species than an ecosystem with lower biodiversity	Elton (1958); Levine & D'Antonio (1999)
Darwin´s naturalization	Alien species that are phylogenetically distantly related to resident species are more likely to be successful than those closely related	Daehler (2001); Darwin (1859)
Disturbance	The invasion success increases in higher disturbed ecosystems	Elton (1958); Hobbs & Huenneke (1992)
Enemy release	The absence of natural enemies (e.g. competitors and predators) in the alien range increase invasion success	Keane & Crawley (2002)
Evolution of increased competitive ability	After having been released from natural enemies, alien species will allocate more energy in growth and/or reproduction, which makes them more competitive	Blossey & Nötzgold (1995)
Fluctuating resource	Pulses of resources, due to an increase in supply or to a decrease in use, enhance the invasibility of communities	Davis et al. (2000)
Limiting similarity	Successful invaders are functionally distinct from species in the recipient community	MacArthur & Levins (1967)
Novel weapons	Alien species have competitive advantage against native species because they possess traits (e.g. biochemical compounds) that are new to the recipient community	Callaway & Ridenour (2004)
Propagule pressure	A high propagule pressure of alien species (i.e. high supply and frequency of introductions) increase invasion success	Lockwood, Cassey & Blackburn (2005)
Tens rule	Approximately 10% of species successfully take consecutive steps of the invasion process	Williamson & Brown (1986)

was published in 2010, revised in 2012, and has cataloged 99 IAS (Resolução CONSEMA 08/2012). Rio Grande do Sul published the official list in 2013 and included 79 species (Portaria SEMA 079/2013). However, there is a lack of studies integrating the information for the *Campos Sulinos* as a whole region and sharing the progress, challenges, and difficulties of IAS management across the three states. The dramatic loss of natural grasslands in the region (Baeza et al. 2022), and the current threats to the remaining areas due to biological invasions, make it essential to continue moving forward for improving management actions.

The success of invasion results from the combination of three main components: (i) the introduction effort (i.e., *propagule pressure*), (ii) the capacity of a species to invade (i.e., *invasiveness*), (iii) and the susceptibility of the recipient community to be invaded (i.e., *invasibility*; Richardson and Pyšek 2006). Although it is difficult to generalize, there are some characteristics that have been associated with invasiveness across different taxa, such as high genotypic and phenotypic plasticity, rapid growth, high and early fecundity, and fertility (Baker 1965; Rejmánek and Richardson 1996). For instance, the invasiveness of *Eragrostis plana*, one of the most abundant invasive alien grasses in Rio Grande do Sul (Guido et al. 2016), has been associated with the high production of seeds that germinate faster than natives

(Guido et al. 2017), a great competitive ability (Guido et al. 2019), resistance to adverse conditions (Guido et al. 2016), and livestock avoidance (Bremm et al. 2016). However, which traits favor invasion depend on the difficulties the species must overcome in the alien range, and therefore, the study of community invasibility is also necessary for understanding the process.

Several hypotheses have been proposed to explain the complex relationship between the invaders and the *recipient community* to explain the *level* and *patterns of invasion* across regions (see Catford et al. 2009; Enders et al. 2020). The hypotheses form the theoretical–conceptual understanding of biological invasions by highlighting the relative importance of certain factors that influence propagule pressure, invasiveness, and/or community invasibility (Catford et al. 2009). As many hypotheses share some similarities, some of them have been more relevant than others (Enders et al. 2020). In Box 19.2, we present a set of these hypotheses, linking some of them to the key factors of invasion developed below.

19.2 Distribution of Invasive Alien Plants and Animals in the *Campos Sulinos*

19.2.1 Data Collection

We used the National Invasive Alien Species Database (bd.institutohorus.org.br) to show general patterns about IAS in the *Campos Sulinos* region. The database includes species that are present in Brazil, with at least one occurrence record, and species that are currently naturalized in Brazil but invasive elsewhere. For this study, we only considered plants and animals with occurrence records within the limits of the *Campos Sulinos* region, and deliberately excluded marine organisms. For each species, we collected data about: (i) inclusion in the IAS official list of the states, (ii) origin (Africa, Asia, Australasia, Central America, Europe, North America, South America, or unknown); and (iii) the main reported human uses (plants: agriculture, forestry, forage, horticulture, none, others; animals: apiculture, aquaculture, hunting, food, pet, none, others).

The occurrence records for each IAS were obtained from two major databases: the national database of the Horus Institute for Environmental Conservation and Development, and the international platform of the Global Biodiversity Information Facility – GBIF (https://doi.org/10.15468/dd.9xa2x7). Additional occurrence records were requested for two environmental agencies: the State Secretariat for the Environment of Rio Grande do Sul (SEMA-RS) and the Biodiversity Authorization and Information System (SISBio/ICMBio; Supp. Table S19.1). We only considered occurrence records with geographic coordinates or municipalities inside the *Campos Sulinos*. The records for each IAS were rasterized into cells of 5 arc minutes resolution (ca. 8.3 × 8.3 km), resulting in 3175 total cells for the whole region. We obtained the total IAS occurrence records and the percentage of invaded cells for the region (number of cells that present at least one IAS/total number of grid cells). For each IAS, we calculated the percentage of records the species represented (number of records of the IAS/total number of records) and the percentage of cells the species was registered (number of cells the IAS occurred/total number of cells in the *Campos Sulinos*). We also obtained the total number of IAS per grid cell (i.e., IAS richness) to develop maps of IAS richness for evaluating invasion distribution patterns. Data processing and maps were performed in R environment (R Core Team, 2020) using the packages "rgbif" (Chamberlain et al. 2021) for acquisition of GBIF occurrences, "rgdal" (Bivand et al. 2021), "rgeos" (Bivand and Rundel 2020) and "raster" (Hijmans 2021) for geospatial analysis and "maps" (Becker and Wilks 2018) for mapping.

19.2.2 Results and Interpretation

We found that 70% of the grid cells inside the *Campos Sulinos* were invaded by at least one IAS, representing 9465 records across the region. A total of 184 IAS were registered (Suppl. Table S19.2), of which 46 were animals (41% of the records) and 138 were plants (59% of the records). Some of these IAS are shown in Fig. 19.2. Rio Grande do Sul was the state with the largest number of IAS (175 species, 72 of them exclusive), followed by Paraná with 95 species, and Santa Catarina with 70 species (Fig. 19.3). In general, most species had low occurrences (<1% of records), and only a few of them had higher values (Suppl. Table S19.2).

The highest occurrence records for plants were for *Eriobotrya japonica, Tradescantia fluminensis, Cirsium vulgare, Syngonium podophyllum, Christella dentata, Tradescantia zebrina, Impatiens walleriana, Eragrostis plana, Melinis repens*, and *Lonicera japonica* (Fig. 19.4a; Suppl. Table S19.2). The records of these plants were mainly from Rio Grande do Sul (>70% of the cells; Suppl. Table S19.2). The most represented families of plants were Poaceae (27 species) and Fabaceae (22 species). Regarding animals, those with the highest number of records were *Passer domesticus, Bubulcus ibis, Canis lupus, Sus scrofa, Lepus europaeus, Columba livia, Felis catus, Apis mellifera, Aedes albopictus*, and *Axis axis* (Fig. 19.4b; Suppl. Table S19.2). The records of these species were also concentrated in Rio Grande do Sul (>70% of the cells were in this state). Terrestrial vertebrates represented the higher proportion of invasive alien animals (44%), followed by invertebrates (30%) and aquatic vertebrates (26%). The most represented families of animals were Cyprinidae and Muridae, both with three species each.

We note that some species with high number of occurrences are not included in the official lists of the IAS of the *Campos Sulinos* region. For example, the plants *Cenchrus echinatus, Cyperus rotundus, Syngonium podophyllum*, and *Tradescantia fluminensis*, which had records in Rio Grande do Sul, Santa Catarina and Paraná (Suppl. Table S19.2), are not mentioned in any of the official lists. Although this divergence can be explained by the frequency the information is updated, since the

Fig. 19.2 Some invasive alien plants and animals with occurrences in the *Campos Sulinos* region (see also Suppl. Table S19.2)

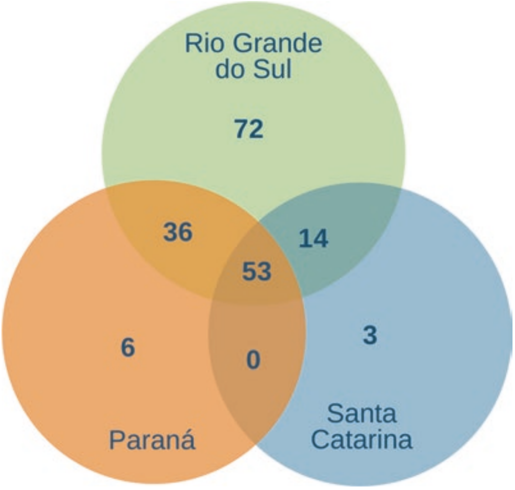


Fig. 19.3 Venn diagram with the number of invasive alien species (animals and plants) exclusive and shared in each state of the *Campos Sulinos* region (Rio Grande do Sul, Santa Catarina and Paraná). For the species list, see Suppl. Table S19.2

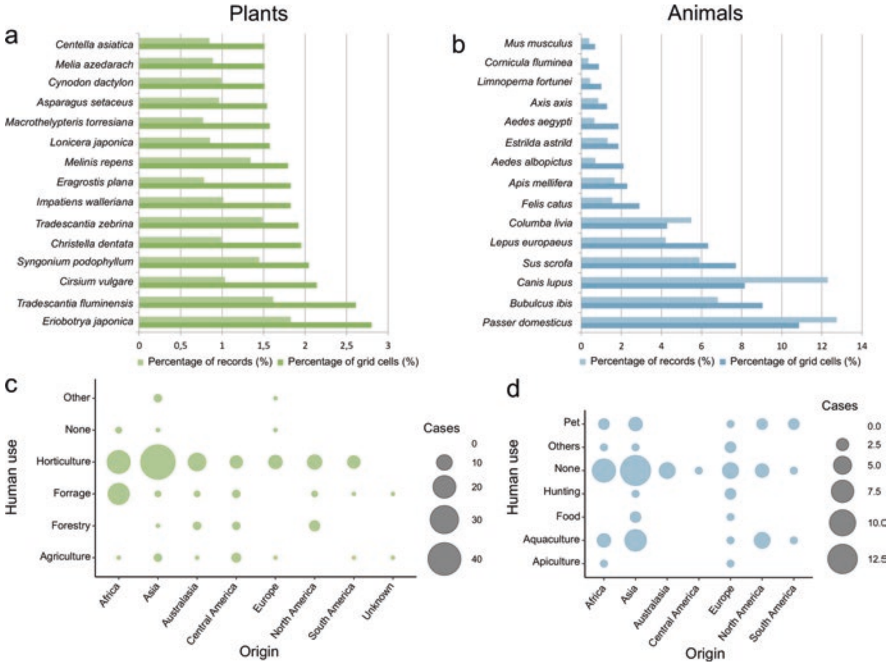


Fig. 19.4 Invasive alien species with the highest values of records (i.e., percentage of records) and occupied area (i.e., percentage of grid cells), separated for plants (**a**) and animals (**b**) in the *Campos Sulinos*. The species with the highest values are shown. Plants (**c**) and animals (**d**) were classified according to their human use and origin (number of cases). Note that one species can have more than one origin and/or use

national database is more constantly revised than the official lists, these species should be monitored to evaluate their further inclusion. The species *Aedes albopictus, Acacia podalyriifolia, Rattus norvegicus, Canis lupus*, and *Felis catus* are already included in the official list of Santa Catarina and Paraná states, but are not considered invasive in Rio Grande do Sul, despite occurrences in this state. We recommend evaluating the inclusion of the bird *Sturnus vulgaris* in the Rio Grande do Sul official list, as it is considered invasive in border countries (Uruguay and Argentina). We call attention to the records of *Bubalus bubalis, Apis mellifera*, *Eragrostis plana*, and *Senecio madagascariensis* in Santa Catarina, as these species are already invasive in Rio Grande do Sul and Paraná, but are not included in the Santa Catarina official list.

Most of the IAS with records in *Campos Sulinos* are from Asia and Africa, and there is an association between this origin and the type of human use. Many of the invasive alien plants are used for horticulture, introduced in Brazil for human consumption and/or ornamental purposes for gardening (Fig. 19.4c). Some examples are *Rubus* spp., *Lonicera japonica, Hovenia dulcis*, and *Ligustrum lucidum* (Suppl. Table S19.2). These results are in line with other studies which have also shown similar patterns and awareness about alien flora in Brazil (Zenni 2014), and in particular in the *Campos Sulinos* region (Fonseca et al. 2013; Rolim et al. 2014). The ornamental horticultural trade has been recognized as the main pathway for plant invasions worldwide since many species can escape from cultivation and have the potential to release in nature (Dehnen-Schmutz et al. 2007). The demand for ornamental plants is driven by consumers in search for attributes (e.g., fast growth) which are often related to invasiveness (van Kleunen et al. 2018). The horticultural industry generally ignores native flora and seeks to meet the demand by importing or breeding alien plants. This highlights the importance of valuing the beauty of native flora and encouraging its use (Rolim et al. 2021), preventing introductions that are not essential for human well-being. Moreover, an important group of invasive alien plants were introduced from Africa to forage production for cattle, such as *Melinis repens* and *Urochloa decumbens* (Fig. 19.4c; Suppl Table S19.2), although many native species are known for their high forage value (Nabinger and Dall'Agnol 2020).

Most animal introductions were probably unintentional transports, since a large number of species were not identified with any human use (Fig. 19.4d). However, by separating into terrestrial vertebrates, aquatic vertebrates, and invertebrates, we found some introduction patterns. Terrestrial vertebrates, such as *Amazona aestiva, Callithrix penicillata, Canis lupus,* and *Felis catus,* were mostly intentionally introduced as pets. Regarding invertebrates, only *Apis mellifera* was identified with human use (apiculture), whereas all the other species were classified as none use, suggesting unintentional introduction pathways. Aquatic vertebrates were mostly associated with aquaculture trade for human consumption, such *Cyprinus carpio, Oreochromis niloticus*, and *Micropterus salmoides* (Suppl. Table S19.2). Thus, in summary, most of the terrestrial and aquatic vertebrates were deliberately transported for different human uses, whereas invertebrates were mainly unintentionally introduced.

Regarding the spatial distribution, although for many cells there were no records (923 cells; gray area of the maps), a high number of IAS can be observed across some regions (Fig. 19.5). Most of the cells had few IAS (1–3 species), but areas closer to major cities, such as Rio Grande, Pelotas, Porto Alegre, and Curitiba, were

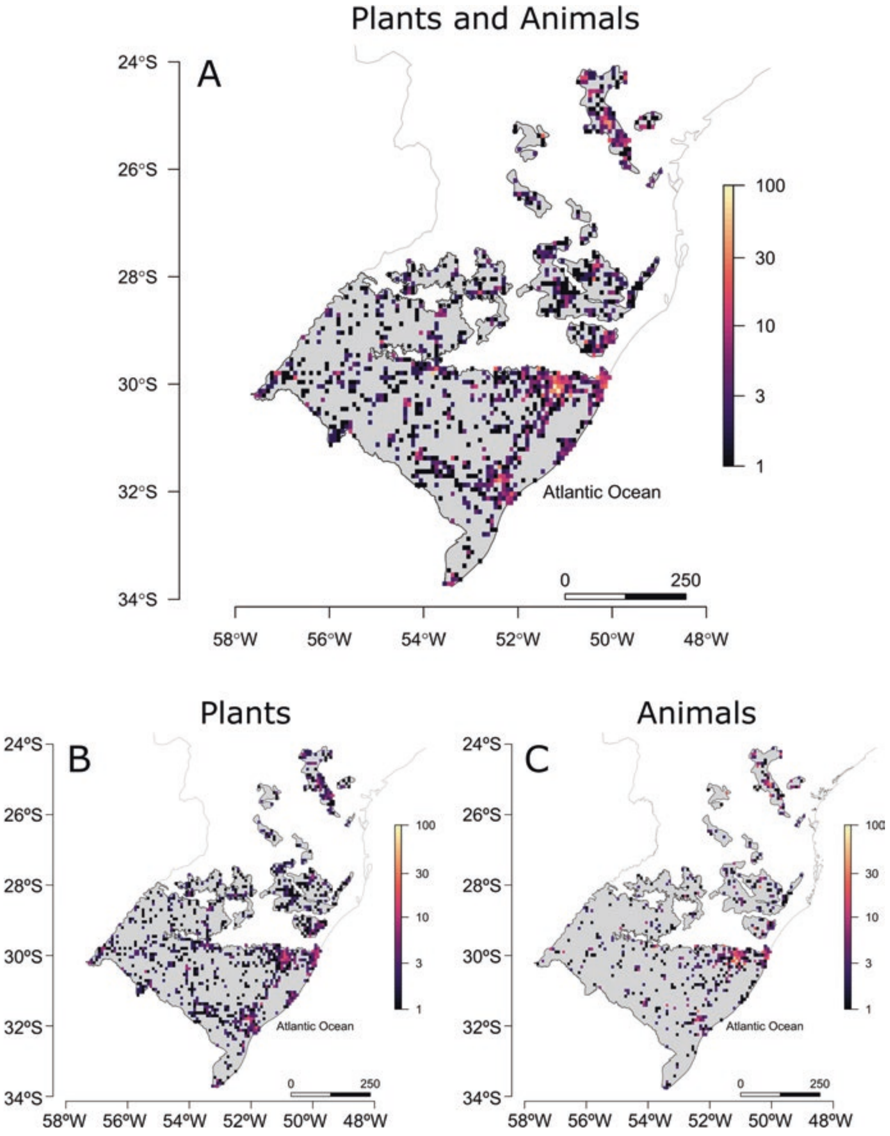


Fig. 19.5 Number of invasive alien plants and animals (**a**), only plants (**b**), and only animals (**c**) per grid cell (1–100 species per cell of 8.3 × 8.3 km) in *Campos Sulinos*. Gray area indicates that there is no occurrence record

richer (>10 species; Fig. 19.5). This highlights the human influence on the invasion process, not only by transporting organisms to the places where we live, but also by promoting suitable conditions for invasion to be successful (see key factors of invasion below). The case of animals reveals how important actions are for preventing non-desirable introductions, and for adequately evaluating the cost–benefit outcomes of intentional transports. Moreover, the importance of residence time in biological invasions has been shown in several other cases (Pyšek and Jarosik 2005), as the longer a species has been present, the more likely it is to establish. However, for most of the IAS in the *Campos Sulinos*, there is no information about the introduction date, thus we cannot disentangle all the causes of the observed pattern.

Understanding the geographical distribution of IAS is important to know which are the most frequent species and where are the most invaded areas. This knowledge can help to identify source regions, as well as vectors and routes that may help to guide management plans. Furthermore, it could be useful to prioritize resource allocation for selective prevention, early detection, and rapid response strategies. Nevertheless, the results presented here should be taken with caution, since the data may include biases as species record effort is not equal across the region (e.g., Hughes et al. 2021). For instance, the invasion level of some areas may be underestimated, since the absence of IAS could either mean lack of information (e.g., inaccessible grid cells where there is no data of the level of invasion) or a non-invaded cell (where the level of invasion is zero). At the same time, for more accessible areas (closer to cities and roads), there may be more occurrence records which can result in an overestimation. Furthermore, it is possible that part of the occurrence records does not indicate a biological invasion, as the GBIF database does not make such a distinction. For example, many alien plants that are cultivated in urban areas, such as gardens and street margins, and registered in the database have the potential to invade natural systems in the near future. We encourage researchers, stakeholders and managers to include IAS records on databases to continue approaching the reality of this problem.

19.3 Key Factors and Impacts of Invasions

19.3.1 Factors of Invasion

For understanding the distribution patterns of invasions, much research has focused on identifying the major factors that enhance the probability of alien species to be transported, introduced, established, and spread. Besides propagule pressure, the abiotic (e.g., environmental conditions and resource availability) and biotic factors (e.g., species interactions) control different barriers (survival, reproduction, and dispersal) that affect the progression of the invasion stages (Fig. 19.1; Theoharides and

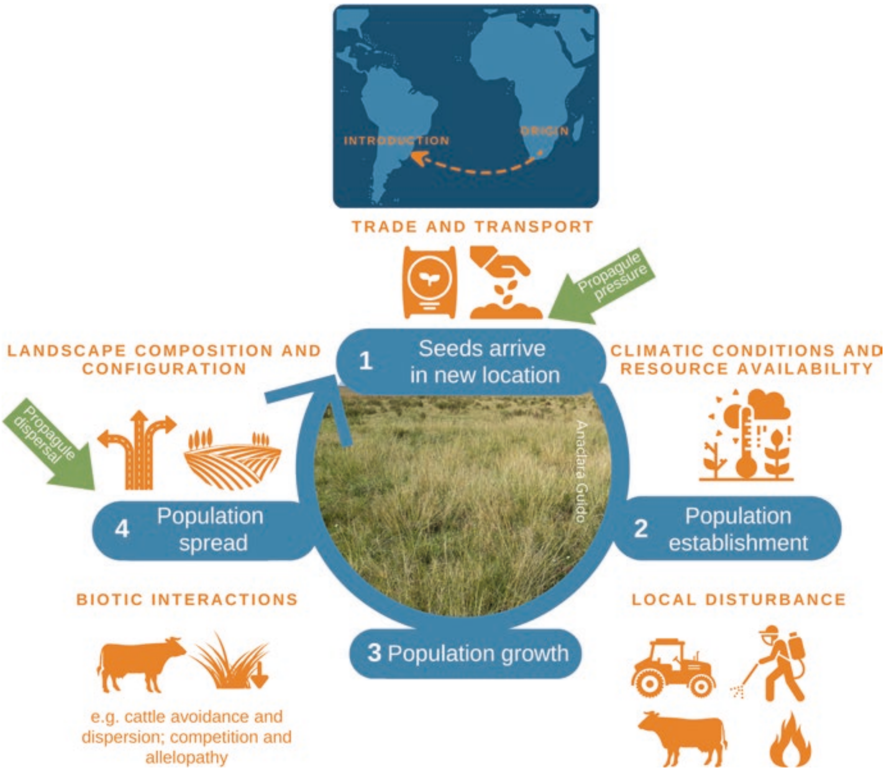


Fig. 19.6 Key factors that promote the invasion of *Eragrostis plana* in *Campos Sulinos* grasslands

Dukes 2007; Catford et al. 2009). The species *Eragrostis plana* is used here as an example to present some factors that promote its invasion in *Campos Sulinos* grasslands (Fig. 19.6).

19.3.1.1 Propagule Pressure

Human activity, such as agriculture, horticulture, and other trades, can shape the early stage of invasion by determining the number of species and/or individuals introduced, as well as and the number of introduction attempts (Lockwood et al. 2005). For instance, the transport of a species into a new region is influenced by socioeconomic and cultural processes that define the manner by which a species is carried (i.e., *transport vector*) and the route between the source and release locations (Lockwood et al. 2007). This pathway could be intentional or unintentional as a result of commodity, vector movements or through natural dispersal (Hulme et al. 2008), which would determine the abundance and rate at which species are introduced to new localities (Lockwood et al. 2005, 2009; see the *Propagule pressure hypothesis* in Box 19.2). For the *Campos Sulinos*, many intentional transports of alien species were shown (Fig. 19.4), but some have unknown causes of introductions, which hinders identifying source regions and vectors. Unintentional introductions can occur in ships' cargo, in seed stocks, or with livestock and travelers from other regions (Mack and Lonsdale 2001). For example, the invasion of the bivalve *Limnoperna fortunei* in South America started with the transport of ballast water from ships trading with Southeast Asia in the Río de la Plata estuary (Darrigan and Pastorino 1995). Therefore, the transit of human-mediated vectors (land, sea, or aerial) has been considered a proxy of propagule pressure and dispersal, as the more abundant and often a vector is transported into an area, the more likely an organism will be carried.

Moreover, human activity at the landscape scale has been considered a proxy of propagule arrival, as it could be the cause of species dispersal by overcoming natural barriers across and/or within regions (With 2002; Theoharides and Dukes 2007). For example, human-built corridors, such as roads, can enhance the propagule pressure in some localities and disperse IAS across regions (Vilà and Ibáñez 2011). In *Campos Sulinos* grasslands, the level of the invasion by *Eragrostis plana*, *Cynodon dactylon*, *Senecio madagascariensis*, and *Ulex europaeus* (see Fig. 19.1) was positively related to the density of roads and urban areas, which probably promote their dispersal across Rio Grande do Sul (Cordero et al. 2016; Guido et al. 2016).

19.3.1.2 Environmental Conditions and Resource Availability

Invasive alien species' survival, growth, and reproduction depend on suitable environmental conditions (e.g., precipitation and temperature ranges) and resource availability (e.g., nutrient level). At a regional scale, climate sets the broad limits of species distribution, and if environmental conditions are not suitable, the invasion fails immediately during the introduction stage (Fig. 19.1). Ecological niche models using bioclimatic variables are often used to predict the potential distribution of IAS worldwide (e.g., Guisan et al. 2014; Liu et al. 2020). For instance, climate matching, combined with intentional captivity or cultivation of alien species, greatly increases the likelihood to escape and establish in the wild. This was the case of *Lithobates catesbeianus* (bullfrog), which was intentionally introduced in southern Brazil in 1935 for aquaculture (Both et al. 2011). Nowadays, its populations are widely spread across Brazil, as individuals escaped captivity and were released by farmers due to the low economic gains, finding suitable climate conditions for survival and reproduction (Nori et al. 2011). However, similar climate conditions could result in different levels of invasion due to other interacting abiotic factors that operate at finer scales (González-Moreno et al. 2014). For example, resource availability (e.g., water, light, and nutrients) is a key factor for species establishment, and thus can impose a constraint barrier for survival. According to the *Fluctuating resource hypothesis* (see Box 19.2), temporal heterogeneity in resource availability opens a window of opportunity for species invasion (Davis et al. 2000). Thus, human activities that cause resource enrichment or release increase community invasibility. For instance, nutrient addition (e.g., nitrogen and phosphorus fertilization) and changes in disturbance regime, such as grazing, fire, and mechanical soil disturbance (e.g., plowing), are important factors that enhance invasion success of plants in the *Campos Sulinos* by modifying the availability of limiting resources (see, e.g., in Fig. 19.6). A long-term experiment in Uruguay showed that adding alien legumes and phosphorus to natural grasslands, a common practice to enhance forage for cattle in the region, increased dominance of the invasive grass *Cynodon dactylon* in an irreversible way (Pañella et al. 2022). Moreover, disturbances that operate at different spatial scales, from landscape context (e.g., habitat fragmentation) to local regimes (e.g., forage management), are key factors shaping the level of invasion across ecosystems (see *Disturbance Hypothesis* in Box 19.2). For example, the abundance of *Eragrostis plana* was positively related with the loss of grassland cover in the landscape (Guido et al. 2016) and overgrazing regime at the local paddock (Baggio et al. 2018; Fig. 19.6).

19.3.1.3 Biotic Interactions

During the stages of the invasion process, alien species are also influenced by biotic interactions among the species from the recipient community, which can facilitate or impede their success (Elton 1958; Mitchell et al. 2006; Traveset and Richardson 2020). Negative interactions in the native range, such as predation and competition, can be less intense in the alien range (see *Enemy release hypothesis* in Box 19.2), and in exchange, IAS encounter new organisms they did not have previous interactions with. Resident species can limit the invasion by affecting their survival, growth, and reproduction, which constitute the main mechanisms of biotic resistance to invasion (Elton 1958; Levine et al. 2004). The classical biotic resistance hypothesis states a negative relationship between the diversity of the recipient community and invasibility, suggesting that more diverse communities are less susceptible to invasion, mainly due to the efficiency in the use of limiting resources (see *Biotic resistance hypothesis* in Box 19.2; Elton 1958). Moreover, functional species composition is also important, as resident species that share similar traits with the invader are likely to compete strongly by niche overlap assumptions (see *Limiting similarity hypothesis* in Box 19.2; MacArthur and Levins 1967).

On the one hand, positive interactions with native species can make the recipient community more susceptible to invasion (Traveset and Richardson 2014, 2020; Aslan et al. 2015). For instance, the establishment of plants can be facilitated through mutualistic interactions with belowground microorganisms which may enhance IAS survival and persistence (Nuñez and Dickie 2014; Menzel et al. 2017). Moreover, pollination and seed dispersal between IAS and resident species is essential for plants overcoming barriers to successfully invade. The reproduction barrier can be overcome by enhancing diaspores production, and dispersion can be succeeded by assisting propagules to colonize distant areas (Traveset and Richardson 2011, 2014; Aslan et al. 2015). The consideration of biotic interactions in invasion biology has facilitated a better understanding of the mechanisms that allow (or not) IAS to integrate recipient communities. For example, across the *Campos Sulinos* region, birds and cattle have been associated with *Ligustrum lucidum* and *Eragrostis plana* dispersal, respectively, through the consumption of their reproductive structures (Marciniak 2015; Minervini and Overbeck 2021).

As biological invasions are context-dependent in space and time, and alien species might only become invasive when certain propagule pressure, biotic, and abiotic factors are met, it is important to consider these driven factors as interactive, and not dissociated, conditions (Heger and Trepl 2003). For example, climatic events (e.g., droughts) and human-mediated disturbance (e.g., overgrazing) can cause fluctuations in resource availability through abiotic (e.g., space and light availability) and biotic process (e.g., changes in community composition and diversity), altering different constraints that may (or may not) lead to a successful invasion.

19.3.2 Major Impacts of Invasion

Invasive alien species are among the five most significant global drivers of biodiversity loss (IPBES 2019), affecting the conservation of natural resources and human well-being (Blackburn et al. 2014). The *Campos Sulinos* region is not an exception. Invasion impact can be evaluated by adopting three dimensions: range, abundance, and the per-capita or per-biomass effect of the invader (Parker et al. 1999). However, the impact can vary in relation to the attributes of recipient ecosystems and the invading species, and the outcomes are highly dependent on human level perception, thus objective assessments have been challenging. An attempt to assess the impact through standardized approaches, the Environmental Impact Classification for Alien Taxa (EICAT; Blackburn et al. 2014; Kumschick et al. 2020) and the Socio-Economic Impact Classification for Alien Taxa (SEICAT; Bacher et al. 2018), has emerged by separating the environmental and socioeconomic impacts. These protocols are receiving international support and have been recently used by the IUCN Red List of Threatened Species (IUCN 2020a, b). In this section, we focus on describing negative impacts of invasion, dividing them into two major groups, (i) environmental impacts, which consist of a significant change in an ecological pattern or process (ii), and socio-economic impacts, which are directly affecting human well-being. The invasive alien species *Eragrostis plana* is used as an example to explain the different impacts in the *Campos Sulinos* (Fig. 19.7).

19.3.2.1 Environmental Impacts of Invasion

Environmental impacts could be assessed at different levels of biological organization (i.e., individual, population, community, and ecosystem) which involves many processes behind. At an individual level, IAS can alter the growth of resident

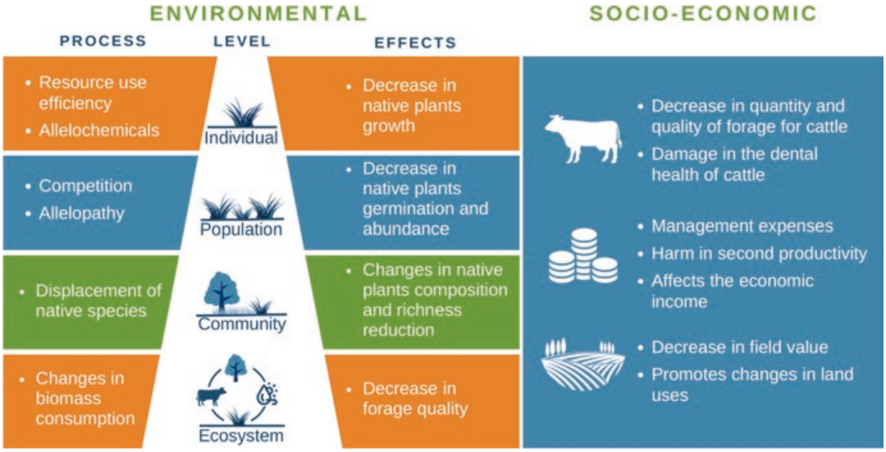


Fig. 19.7 Environmental and socio-economic impacts of *Eragrostis plana* invasion. Environmental impacts are distributed according to ecological levels. (Source: synthesis of results from Guido and Pillar (2017), Guido et al. (2017, 2019, 2021) and Dresseno et al. (2018))

organisms, which are frequently easy to measure and to extrapolate to higher level impacts. For instance, a pair-wise experiment in the *Campos Sulinos* showed that *Eragrostis plana* has negative effects on the growth of neighboring native plants by reducing their height, and the production of tillers, leaves, and biomass (Guido et al. 2019; Fig. 19.7). These impacts can often be translated into declines in rates of reproduction and survival, which affect population dynamics. For example, a decrease in native plant abundances with increasing cover of *Eragrostis plana* has been shown (Guido and Pillar 2017; Dresseno et al. 2018; Fig. 19.7). There are many ecological mechanisms by which the invader impacts populations, such as competition for resources (Crawley 1990), predation (Medina et al. 2014), chemical or physical inhibition of growth (Grove et al. 2012), or disruptions of mutualistic networks (Traveset and Richardson 2011, 2014). For instance, some invasive alien plants have the potential to release phytotoxins that inhibit the germination and/or growth of native species (Callaway and Ridenour 2004; see *Novel weapons hypothesis* in Box 19.2). This mechanism has been studied for *Eragrostis plana* and *Cynodon dactylon* in the *Campos Sulinos*, as these species showed allelopathic potential that could lead to suppression of neighboring native plants (Favaretto et al. 2015; Guido et al. 2020). However, this isolated process might not be enough for explaining their high invasiveness (Guido et al. 2020), and competition ability is probably the most important mechanism beyond their invasion success (see *Evolution of increased competitive ability hypothesis* in Box 19.2; Guido et al. 2019). Another example is the invasive alien frog *Lithobates catesbeianus*. Its calls impact native amphibians by changing their acoustic signals, decreasing the probability of mate selection and thus reproductive success (Medeiros et al. 2017). This species also impacts native amphibians through predation and disease transmission by the spread of the fungal *Batrachochytrium* spp. (Oda et al. 2019; Ruggeri et al. 2019).

Invasion alters the structure of recipient communities, as they often promote changes in species composition, richness, diversity and/or dominance of resident species (Crystal-Ornelas and Lockwood 2020). For example, the invasive alien fishes *Oncorhynchus mykiss* and *Micropterus salmoides* impact native ichthyofauna by reducing the richness, abundance, and/or biomass in rivers of Rio Grande do Sul state (Sosinski 2004). In southern Brazilian grasslands, the invasion of *Eragrostis plana* reduces the number of species in plant communities, as it has been observed that 30% of *E. plana* cover displaces in average 10 native plants (Guido and Pillar 2017). As a consequence, much of these changes have been associated with biotic homogenization of recipient communities (taxonomic, functional, and/or phylogenetic), as the expansion of alien species can replace native biota, diminishing floral, and faunal distinctions among regions (Olden 2006).

Recipient community changes generally have consequences on the cycles of matter and on the energy flow of systems, and thus biological invasion has major impacts on ecosystems functioning (Simberloff 2011; Vilà and Hulme 2017). Invasion can alter trophic networks, ecosystem productivity, nutrient cycling, hydrology, habitat structure, and various components of disturbance regimes (e.g., Ehrenfeld 2010; Damasceno et al. 2018; Damasceno and Fidelis 2023). For example, *Eragrostis plana* invasion alters biomass consumption by livestock on grasslands due to its high values of leaf toughness (Guido et al. 2021; Fig. 19.7). Grazers avoid its consumption by overgrazing native species, which, in turn causes a positive feedback of invasion (Bremm et al. 2016; Guido et al. 2021). Thus, invasion can also alter local disturbance regimes (Mack and D'Antonio 1998), affecting resident species regeneration and enhancing invasibility, which might cause positive feedback of the invasion process (Damasceno and Fidelis 2020; Guido et al. 2021). For example, some invasive alien plants are more flammable than natives, and thus can enhance flame height and temperature, mostly due to changes in fuel properties (e.g., more percentage of dead biomass and lower fuel moisture), leading to more severe fires (Gorgone-Barbosa et al. 2015). As a consequence, native vegetation may be negatively affected, and invasion probability increases. Some IAS in the *Campos Sulinos*, such as *Ulex europaeus, Melinis minutiflora, Pinus* spp., and *Urochloa decumbens* are usually pyrophytic and highly flammable (Gorgone-Barbosa et al. 2015; Pausas et al. 2012; Cornwell et al. 2015), changing local fire behavior.

19.3.2.2 Socio-Economic Impacts of Invasion

Invasive alien species can impact many ecosystem services and thus affect the activities related to human well-being, such as (i) agriculture, horticulture, livestock, and forestry production; (ii) health; (iii) tourism and leisure; (iv) and infrastructure and buildings (Nentwig et al. 2016; Vilà et al. 2019). Adelino et al. (2021) recently estimated the economic costs of biological invasions and showed that *Aedes* spp., *Limnoperna fortunei* and *Eragrostis plana* were the costliest IAS in Brazil by affecting different market sectors. For example, agriculture was the most impacted activity with an economic cost estimated at USD 39.61 billion, followed by health with USD 665.85 million, which are both attributed to invasion damage and also management strategies cost (Adelino et al. 2021).

Particularly in the *Campos Sulinos*, the effects of IAS on agriculture and livestock production are remarkable. The invasion of *Eragrostis plana* impacts extensive cattle production, one of the main economic activities in Pampa biome, by reducing forage palatability, damaging cattle dental health, and thus affecting secondary production and economic incomes (Medeiros and Focht 2007; Guido et al. 2021; Fig. 19.7). In addition, the value of invaded grasslands can considerably diminish, and might also promote changes in the use of the land by transforming natural grasslands into agricultural or forestry uses (Ferreira and Filippi 2010; Fig. 19.7). Another example is the invasion of the wild boar *Sus scrofa,* which has caused economic and social conflicts mainly due to damage to the agricultural sector. In southern Brazil, wild boars could damage 5–30 ha/year of corn crops (Salvador 2012), and the impact caused is worst for small farmers (<50 ha), who may lose the entire planting for a year (Batista 2015). Moreover, there is the risk of disease outbreaks, as wild boar could be reservoirs of diseases that impact commercial pig farming (Salvador and Fernandez 2017).

Moreover, the invasion by *Limnoperna fortunei* (Fig. 19.2) is an example of notable impacts on infrastructure and buildings, as its settlement affects water processing plants, power plants (nuclear, hydroelectric, thermal), refineries, steel mills, fish culture facilities, water transfer canals and aqueducts, and watercraft (Boltovskoy and Correa 2015). Furthermore, many IAS are vectors of human diseases and thus pose a serious threat to public health. This is the case of *Aedes* spp., which in Brazil is responsible for the spread of at least three different arboviruses (i.e., Dengue, Zika, and Chikungunya) that threaten human health (Marcondes and Ximenes 2015), costing millions of reais (BRL) with insecticides, larvicides, and medical care (Teich et al. 2017).

19.4 Prevention and Control: Options and Challenges for Management

Brazil recognizes that biological invasion is a problem that needs to be addressed with required management actions (Zenni et al. 2016). Some initiatives have been implemented to try to decrease the impacts, to prevent new introductions and to eradicate and control already established IAS populations. Prevention, early detection, and rapid response to IAS in Brazil are foreseen in the National Strategy for Invasive Alien Species (Resolução CONABIO n° 7 – 2018). Several national action plans have been implemented by the *Instituto Chico Mendes de Conservação da Biodiversidade* since 2012, covering different groups of species and ecosystems (ICMBio 2019). Complementarily, there has been an effort of other organizations, such as Horus Institute for Environmental Conservation and Development, The

Nature Conservancy (TNC), Inter-American Biodiversity Information Network (IABIN), as well as from the Global Invasive Species Program (GISP), to provide information about IAS in Brazil (Zenni et al. 2016).

At the state level, Rio Grande do Sul, Santa Catarina, and Paraná have programs where strategies for IAS management have been proposed. Besides the publication of the official species lists, there are complementary regulations to establish limits of use of IAS. For that, each listed species is categorized into two alternative categories: (I) banned species, or (II) permitted species with regulations for their uses. The first category included species that are prohibited from being transported, raised, released, or translocated, cultivated, propagated by any means of reproduction, trade, donation, or intentional acquisition in any way. An example of this category in the *Campos Sulinos* is *Limnoperna fortunei*, banned across the three states, and for which exists a Federal management program. The second category refers to species that are mostly associated with production systems, and thus can be used under controlled conditions, with restrictions that are subject to specific regulations from each state. An example within this category is *Apis mellifera*, an IAS whose use is restricted for honey production.

Although efforts have been increasing during the last decade, most of the management plans of protected areas in Brazil do not foresee actions concerning IAS with detailed goals, interventions, monitoring plans, budgets, and timelines, indicating the lack of knowledge and training of local managers (Dechoum et al. 2018). Moreover, much of the work has been done independently by several groups, without a complementary action and coordinated agenda within and across the three states, thus the achievement of positive results regarding IAS management has been challenging.

19.4.1 Management Strategies

The management of IAS involves several actions that need to be well defined and prioritized for effective and successful goals (McGeoch et al. 2016; Stone and Andreu 2017). One of the first steps is to assess the stage of the invasion process of the target species (Fig. 19.1), because the more recent the invasion process, the higher the probability to achieve successful results (Ziller et al. 2020). In parallel with the stages and barriers of the invasion, three successive actions form the recommended practices to manage IAS: (1) prevention, (2) eradication and (3) control (Hulme 2006; Blackburn et al. 2011; Fig. 19.1). Which species to manage and where to focus the management effort are the most challenging questions, and thus protocols to guide these decisions must exist (Ziller et al. 2020).

If the target alien species was not introduced yet, but the risk of invasion is identified, management should focus on the *prevention* of introduction in more vulnerable sites (McGeoch et al. 2016; Fig. 19.1). Prevention actions aim to impede the arrival of propagules to a certain location, constituting the most cost-effective intervention. It can be reached by (i) interception of the material; (ii) treating the material that is suspected to be contaminated (e.g., quarantine), and (iii) prohibition of commercialization (Wittenberg and Cock 2001). To be successful, it is crucial to identify the likely vectors and routes involved to establish regulations that limit its introduction. This has been included in the Aichi Biodiversity Target 9 of the Convention on Biological Diversity (CBD), in which the participant countries, including Brazil, must identify and prioritize their pathways of introduction to prevent IAS. In Brazil, the introduction of alien species without official authorization is considered an environmental crime (Federal Law 9.605/1998).

In the *Campos Sulinos*, many invasive alien vertebrates were deliberately introduced and escaped or released into nature (Fig. 19.4). For example, we show that some species were commercialized as pets (e.g., *Canis lupus, Felis catus*, *Estrilda astrid*, and *Trachemys scripta*) and for aquaculture trade (e.g., *Ictalurus punctatus* and *Oreochromis niloticus*). To prevent these cases, risk analysis, considering the risk of establishment, spread, and impact on nature, should be urgently carried out. Only after balancing the risks and the potential advantages, a final decision about proceeding with the importation should be reached (Wittenberg and Cock 2001). Complementarily, the selected species to be imported should have a preventive plan to avoid their release or escape into the wild. In addition, public education is crucial to minimize pet releases by informing the owner of the species characteristics and needs, and also the risk the organism represents to native species.

Moreover, many unintentional introductions in the *Campos Sulinos* concern invertebrates, and thus much effort should be focused on their invasion vectors, which are often associated with international trade and tourism routes. Prevention actions often include a treatment for the suspected introduction vectors (e.g., quarantine, cleaning, thermal shock, and fumigation), based on regulations and laws. For example, to prevent new introductions of aquatic invertebrates (e.g., *Limnoperna fortunei* and *Corbicula fluminea*) by the traffic of ships, the ballast water must be exchanged offshore before arriving at the harbor (IBAMA 2020). In the case of plants, species used for horticulture in the *Campos Sulinos*, and particularly from Africa and Asia, should be more carefully analyzed before introduction, since many of these cases resulted in a biological invasion (e.g., *Tradescantia fluminensis, Lonicera japonica, Melia azedarach*, and *Ulex europaeus*; Fig. 19.4). Besides the importance in carrying out a risk analysis, prevention actions should also focus on sensitizing the population about the value of native vegetation and its potential use. For example, there are many native plants in the *Campos Sulinos* with high potential for forage or ornamental value that are neglected (Rolim et al. 2021) and whose use can prevent further and unnecessary introductions.

Prevention of invasion is not always feasible, since the species is often already introduced, or even established, in the system and *eradication* and *control* actions need to be implemented to limit its spread (Fig. 19.1). Eradication consists in the extirpation of an entire population within a specific area (Pyšek and Richardson 2010; Hulme 2006). However, eradication is not always possible since the connectivity of IAS populations can rapidly increase, hindering early detection and rapid response, and thus successful examples have been challenging worldwide. *Control* aims to reduce the abundance and density of established and/or widespread IAS populations and contain them in an acceptable threshold that minimizes their impact (Wittenberg and Cock 2001; Fig. 19.1). Eradication and control programs have been based on different methods of IAS removal, such as mechanical (e.g., handpicking, pulling, or cutting for plants), chemical (e.g., use of biocides), habitat management (e.g., grazing, mowing, or burning the area), and hunting (Wittenberg and Cock 2001). The selection of one technique, or a combination of them, would depend on the target IAS, the type of system, and the level and time since invasion.

To locally control invasive alien grasses in grasslands, mechanical removal is often used. It can be conducted by manual removal by hand, cutting, or even hoeing of isolated individuals and/or populations. To avoid reestablishment, monitoring and repeated long-term actions are important since species can resprout or germinate from the seed bank (ICMBio 2019). For example, in South Brazil grasslands invaded by *Eragrostis plana*, 4 years of annual removals by different methods (clipping, herbicide, and hand-pulling) were not enough to locally extinguish the species (Guido & Pillar 2017; Guido et al. 2021). Another control strategy is to promote abiotic conditions through management decisions that limit the invasion by affecting the survival, reproduction, or dispersal. For example, when alien C_4 grasses invade areas close to forests under regeneration, shading can control their spread, as many of them are shade-intolerant species (e.g., *Eragrostis plana* and *Cynodon dactylon;* ICMBio 2019). Moreover, management practices like fire can be useful to control species densities, such as of *Melinis minutiflora* and *Ulex europaeus*; although it is not suitable for all invasion foci and could also have non-targets effects (e.g., native species regeneration and reinvasion from the seed bank; Madrigal et al. 2012; Damasceno and Fidelis 2020; Assis et al. 2021). The use of herbicides (e.g., glyphosate) is also a common technique to control invasive alien grasses in the *Campos Sulinos*, such as *Urochloa decumbens* (e.g., Thomas et al. 2018), *Eragrostis plana* (Guido and Pillar 2017), and *Cynodon dactylon*. However, the application of herbicides needs to be carefully evaluated, as its use in protected areas in Brazil is under restriction (ICMBio 2019), and non-target species could be also impacted (Guido and Pillar 2017).

For most species, there is often no single method of control, and the use of combined control techniques may help to reach better results. For example, *Pinus* spp., escaped from cultivation, is one of the most invasive trees in the *Campos Sulinos*. Depending on tree age and time since the invasion, different techniques can be used to manage them. If trees have <4 cm of diameter, fire will exterminate young individuals, which can also be hand-pulled. Adult individuals can be cut at the base of their trunk (e.g., Dechoum et al. 2019), have their bark ringed (at least a ring of 40 cm), or be killed by the combination of the technique of bark ringing and the application of herbicide. When invasion is massive and older in grasslands, a combination of different techniques should be applied, such as cutting of trees and removal of the timber, followed by prescribed fires after 6 months (enough time to dry out all residuals; Durigan et al. 2020). In the case of animals with different development phases, there may be different control methods throughout its life cycle. For example, for *Limnoperna fortunei*, biocides can be used to control larvae, while mechanical methods, such as surface scraping, are applied to adult individuals (IBAMA 2020).

Local management of an IAS should also be complemented by broader actions to contain the spread within and across countries or regions. For that, the identification of the main vectors associated with propagule dispersal is crucial for coordinating actions in neighboring municipalities, states, and countries to integrate and optimize the efforts. Otherwise, a species that is being controlled in one state might reinvade from the border of a neighboring state through water, land, or air traffic. This would require an effective biosecurity approach that builds on knowledge of potential invaders, susceptible systems, and main pathways of spread. Moreover, strategies that promote the conservation of the *Campos Sulinos* at landscape level may reduce the risks of invasions across the region by constraining propagule dispersal of already established IAS (Guido et al. 2016).

Nevertheless, isolated, and short-term practices are often ineffective tools to manage invasions. Long-term planned actions which account for the mitigation of ecological and socioeconomic impacts should be also considered (García-Díaz et al. 2021). For instance, adaptive management can be defined as "learning by doing", involving practices that can be changed according to the results from the management actions (Walters and Holling 1990; Williams and Brown 2016), and not from only one event (Leffler and Sheley 2012). Therefore, monitoring is crucial and should be addressed to (re)evaluate the progress of management planning (Williams and Brown 2016), and thus helping to select the best techniques to be used in each situation (Zalba and Ziller 2007). García-Díaz et al. (2021) suggested six guidelines to help decision makers to plan a long-term management of IAS: (1) map the presence and distribution; (2) investigate the time of residence; (3) evaluate the impacts; (4) identify feasible interventions from an ecological and socioeconomic point of view; (5) detect negative impacts of the interventions; and (6) provide a balance of costs and benefits of interventions and the negative impacts.

19.4.2 Restoration of Invaded Grasslands

Invaded areas have been the focus of ecological restoration programs by assisting the recovery of certain properties that were degraded by invasion (Gaertner et al. 2012). This process involves implementing actions that will set an ecosystem on a trajectory towards a non-invaded reference situation. Most restoration efforts are focused on a succession-based approach for vegetation, where the reestablishment of disturbance and/or physical conditions would be enough for ecosystem recovery (Suding et al. 2004). The recovery of the vegetation structure may cause suitable environmental conditions for the colonization by animals, reestablishing trophic interactions in the ecosystem and thus their main functions (Ruiz-Jaen and Mitchell Aide 2005). However, highly invaded systems often have shifted to a new alternative state by breaching biotic or abiotic thresholds to achieve spontaneous recovery

(Suding and Hobbs 2009; Pañella et al. 2022). Thus, restoring invaded areas has the double challenge of controlling the IAS, which is part of the causes of ecosystem degradation, and also promoting the conditions that make community recovery possible (see Thomas et al. 2023, Chap. 20, this volume).

The isolated control of IAS can be insufficient for achieving long-term restoration goals, since reinvasion (or new invasions) are likely to happen, and invasion may have imposed constraints to achieve native community recovery (D'Antonio and Meyerson 2002). For example, the seedbank of invaded areas can have a high dominance of IAS, and disturbance resulting from control methods can have a positive effect on its germination (Gorgone-Barbosa et al. 2016; Dairel and Fidelis 2020). If there are no active restoration actions after the control of *Melinis minutiflora* in open ecosystems, the area is suitable for *Urochloa* spp. invasion (Damasceno and Fidelis 2020) since this species dominates the seedbank (Dairel and Fidelis 2020). In *Campos Sulinos*, 4 years of continuous removals of *Eragrostis plana* were not enough for degraded grasslands to resemble non-invaded reference grasslands (Guido and Pillar 2017; Guido et al. 2021). In addition, after 50 years of the presence of *Pinus* spp., native species may not be able to regenerate by resprouting from belowground bud banks since these organs suffer a drastic decrease in density (Ferraro et al. 2021). Also, the thick layer of needles does not allow species to reestablish, and even after the removal of the needle layer (by manual removal or fire), bud bank of grasses and forbs may not be enough to guarantee vegetation regeneration (Zanzarini et al. 2019). These results have challenged traditional restoration efforts owing to many different constraints, promoting the search for active strategies for the reassembly of native communities.

Active restoration strategies for revegetation mainly involve native plant reintroduction by sowing, topsoil transfer, seedling transplant, and hay transfer (Vieira and Overbeck 2015). This reintroduction may cover the bare soil and increase biodiversity, which could in turn enhance the biotic resistance to reinvasion (Elton 1958; Schuster et al. 2018). However, studies about active restoration in invaded areas in the *Campos Sulinos* are still scarce (see Thomas et al. 2023, Chap. 20, this volume). One example of positive results is the case of a Brazilian Army reserve in the Pampa region (Rosário do Sul, RS), where a recovery process of the bird community was observed during the initial recovery of a grassland on a site with a history of agriculture (soybean) and further degraded by invasion by *Eragrostis plana* (da Silva and Fontana 2020). However, Thomas et al. (2018) suggest that hay transfer and sowing native grasses had unsatisfactory results to reintroduce species in invaded areas by *Urochloa decumbens*. These examples illustrate that even within the same region, different approaches may be required, depending on the ecosystem affected, the target IAS to manage and the type of degradation that has occurred. Thus, more information is needed to better guide IAS management and active restoration strategies, and particularly in the *Campos Sulinos* region where there are still major gaps of knowledge (Guerra et al. 2020). For instance, it would be helpful to identify which groups of species constrain selected invaders and also promote community reassembly process (Bakker and Wilson 2004; Funk et al. 2008). In addition, since fire and grazing are important factors in the *Campos Sulinos* (Baggio et al. 2021;

Fidelis et al. 2021; Paruelo et al. 2021), restoration plans should also incorporate these natural disturbances as part of the recovery process (Buisson et al. 2019, 2021, 2022; Silveira et al. 2020).

19.5 Invasions under Global Change Scenarios: The Way Forward

The ongoing global scenario, which includes climate and land use changes, is expected to influence biological invasions by affecting propagule pressure, environmental conditions, and biotic interactions. Effects of global change likely will include (1) modification of environmental background conditions, promoting shifts in species distributions, and thus resembling communities; (2) increased probability of extreme climatic events, resulting in greater disturbance and pulses in resource availability; and (3) triggering of human responses to these changes (Bellard et al. 2013; Catford and Jones 2019; Turbelin and Catford 2021). Although there is considerable uncertainty, it is predicted that invasions will increase with rises in temperature and increases in extreme climatic events. IAS are able to shift their niches faster than natives (Wiens et al. 2019), showing a great capacity to adapt to climatic conditions. Moreover, biological invasions are not only a consequence of the ongoing global change but are also one of its interacting main drivers (Sala et al. 2000). Exploring the multifactor effects of global change may improve the predictions and bring more efficient tools to diminish the threats reported to *Campos Sulinos* biodiversity.

In the *Campos Sulinos*, given climate change projections (Marengo et al. 2009), the ongoing land use conversion of natural grasslands (Baeza and Paruelo 2020; Baeza et al. 2022), and the lack of conservation and management efforts (Overbeck et al. 2007), biological invasions would be continuing to increase at alarming rates. For instance, it is one of the South American regions that would increase the number of invasive alien grasses under climate projections (Barbosa 2016). Most of the invasive alien grasses in this region are from tropical areas in Africa, and thus the increment in the minimum temperature may increase the ability of these species to expand their alien ranges.

However, we must understand how complex the process of invasion is and the main mechanisms behind it to manage and predict future invasions. It is important to invest in scientific and technical knowledge to better address the scarcely documented impacts and to project future scenarios. Skills for early detection of invasion processes and rapid response for successful management need to be developed, just as public awareness needs to be improved. The documentation of general patterns of invasion, as provided in this chapter, helps to guide management strategies. For example, as shown in Fig. 19.5, the most invaded areas across the region are associated with higher direct human impact. We call attention to the many areas that have no data, which could be the result of false negatives of invasions, and thus encourage the inclusion of records of IAS in accessible databases. It is important to centralize the information about how, why, where, and by which IAS the *Campos Sulinos* are currently and potentially invaded. Public databases, such as the one used in this chapter, play an important role to collect, centralize, analyze, and update data to move forward.

Finally, studies on biological invasions have been increasing in the last decades in the *Campos Sulinos*. For instance, the region has the advantage of having official lists of IAS for the three states, complemented by some laws and regulations. However, many of the actions have been done independently and in parallel by each state and for several different groups, including scientists, managers, society, and politics (Zenni et al. 2016; Dechoum et al. 2018). A more coordinated and articulated agenda among academia, stakeholders, and people involved across states is needed to integrate, guide, and optimize the efforts and resources for increasing positive results in this challenging scenario. For this, actions should cover the region as a whole to share management responsibilities for the prevention of new introductions, and to eradicate and control the established populations. Biological invasion is caused by human actions; thus we need to raise public awareness, together with government agencies, academia and not-for-profit organizations about the importance of human dimension in the invasion process for better-informed decisions and more effective management and restoration programs. For instance, it would be important to build a unique protocol for the entire *Campos Sulinos* region including (i) the assessment of the current and potential IAS, (ii) priority-setting plan of which species to manage and where, (iii) identification of main pathways of introduction and dispersal, (iv) unify monitoring protocols, (v) investment in scientific and technical knowledge to generate information and develop appropriate skills, (vi) education and people awareness, and (vii) public information systems. With this information, it is possible to enhance the chances of producing large-scale positive results at the lowest cost possible for the whole region.

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Chapter 20
Ecological Restoration of *Campos Sulinos* Grasslands

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20.1 Ecological Restoration and Subtropical Grasslands

Ecological restoration – the process of assisting the recovery of a degraded ecosystem (Society for Ecological Restoration 2004) – has developed to an important field of work in Brazil, and Restoration Ecology, the field of research that underpins it, has equally gained more attention recently. Much of this is related to the activities of the Atlantic Forest Restoration Pact, an initiative that aims to recover 15 million hectares of degraded land in the Atlantic Forest biome by 2050 (Rodrigues 2009). Restoration of non-forest vegetation ecosystems, such as grasslands and savannas that originally cover 27% of Brazil (Overbeck et al. 2022), however, is still less developed (Guerra et al. 2020). Ecological restoration of grasslands in the *Campos Sulinos* region – comprising the grasslands in the states of Rio Grande do Sul (RS), Santa Catarina (SC), and Paraná (PR) (Overbeck et al. 2022) – is a new topic: the

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first larger restoration projects only started in the very recent past. Equally, the research field of Restoration Ecology is new for grasslands in the region; the starting point of the debate might be the paper 'Restoration Ecology in Brazil – Time to Step Out of the Forest', published in 2013 (Overbeck et al. 2013).

The fast conversion of *Campos Sulinos* grasslands to other land uses and their low resilience to severe disturbances make the development of restoration techniques urgent. It is now generally accepted – at least in the scientific community – that the protection of conserved areas is not enough to protect the biodiversity and to maintain ecosystem services and functioning: we need to restore degraded areas (Hilderbrand et al. 2005; Gann and Lamb 2006; Fischer et al. 2021). Previous knowledge from other grassland regions, in particular from temperate Northern Hemisphere grasslands, serves as an important basis for research and practice in ecological restoration in the region. Restoration in the *Campos Sulinos* thus does not start from zero, even though it is necessary to develop techniques, tools, and concepts appropriate to the specific conditions and characteristics of these ecosystems (Overbeck et al. 2013; Silveira et al. 2020). Besides the motivation to restore biodiversity, there are other good arguments for restoration (Holl 2023): economic motivations, such as job and income generation, cultural reasons, and, last but not least, legal obligations. Restoring ecosystems also is an ethical question, as it seeks to leave healthier ecosystems for future generations. Due to the urgency of ecological restoration, the United Nations defined 2021–2030 as the Decade of Ecosystem Restoration. Brazil, with the National Plan for the Recovery of Native Vegetation (*PLANAVEG: Plano Nacional de Recuperação da Vegetação Nativa*, in Portuguese, Brasil 2017) has developed its own ambitious restoration aims: until 2030, 12.5 million hectares of degraded land are to be restored.

Strategies for ecosystem restoration can be classified into two main approaches: passive and active restoration (Holl and Aide 2011; Gann et al. 2019). Passive restoration (sometimes called spontaneous regeneration) considers that upon removing the cause of degradation, the potential for natural recovery is high, as the barriers

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hindering ecosystem recovery are small; thus, there is no need for human interventions. This approach relies on secondary succession and the inherent regeneration capacity of the system after stopping disturbances. Active restoration, however, is necessary when the potential for spontaneous regeneration is absent or low due to strong limitations, such as altered soil conditions, limited dispersal or establishment of target species, and inadequate disturbance regime (Gann et al. 2019). In active restoration, human interventions are used to allow, or at least speed up, the recovery of the ecosystem, ranging from smaller interventions such as changing management and introducing species by planting or sowing to larger interventions with engineering actions, as in the case of degradation by mining. It should be noted, however, that application of the concept of passive restoration, often successfully applied in forest restoration (Crouzeilles et al. 2017), to grasslands is more difficult. Successional processes in *Campos Sulinos* grasslands without any human management lead to woody encroachment and may result in forest expansion (see Müller et al. 2023, Chap. 16, this volume). Thus, active vegetation management is necessary along the restoration process even when the potential for natural recovery is high.

The decision of which approach is more adequate in a specific case depends on the magnitude of the limitation that prevents the ecosystem recovery after a disturbance, but also on ecological processes such as seed dispersal (Holl and Aide 2011; Perkins and Leffler 2018; Gann et al. 2019). The goals, the resources, and the budget available for the restoration project are also important elements to decide which strategy to take (Holl and Aide 2011; Jones et al. 2018). Ambitious goals in a short time require more active interventions than less ambitious goals in the long term.

Subtropical grasslands are highly resilient to fire and herbivory. Both are considered to be endogenous disturbances: over evolutionary periods, they have been important for the maintenance of the structure, dynamics, and biodiversity of many, if not most, tropical and subtropical grasslands (e.g., Bond 2016; Buisson et al. 2019; Veldman et al. 2015, Andrade et al. 2023, Chap. 8, this volume). The reason for this resilience is the presence, in many species, of belowground structures (e.g., rhizomes, lignotubers, xylopodia that form the bud bank in the soil), that allow for plant survival during and recovery of biomass after a disturbance event (Bond 2016; Fidelis et al. 2009; Veldman et al. 2015). Fire and herbivory should thus not be considered direct drivers of degradation processes, unless their frequency or intensity is far out of the range under which the system has evolved. They may even be interesting and necessary tools in grassland restoration (Buisson et al. 2019; Silveira et al. 2020). Moreover, remnant areas of native grasslands that are managed with grazing and/or fire can be used as reference ecosystems that are needed to inform baseline values of target ecosystem characteristics and functioning. In contrast, exogenous disturbances, such as vegetation suppression for use as agricultural land or silviculture and the invasion of alien species, have strong impacts on biotic and abiotic components of subtropical grasslands, especially when they affect belowground structures and processes (Buisson et al. 2019). After such exogenous disturbances, resilience is likely low, and ecological restoration is thus challenging: it requires active interventions, such as restoring soil conditions, introducing native species, and controlling invasive species (Buisson et al. 2021). These activities will be at the center of this chapter. We start with a short overview of the conservation and degradation of *Campos Sulinos* grasslands, discuss the legal and social contexts of their restoration, and then present the state of the art of ecological restoration in the region. In the closing section, we suggest ways forward to advance in the restoration of grasslands in the region.

20.2 Conservation State and Threats of *Campos Sulinos* Grasslands

As mentioned earlier, fire and grazing are key factors driving ecological processes in the *Campos Sulinos*, and appropriate management is thus of high relevance for the conservation of these grasslands. In general, exclusion of these disturbances leads the community to be dominated by tall tussock grasses and to woody species encroachment, resulting in species-poor plant communities due to drastic losses of the highly diverse forbs component and prostrate grasses (Boldrini and Eggers 1996; Guido et al. 2017; Sühs et al. 2020). After long-term exclusion of disturbances, the bud bank also diminishes, especially of forbs (Fidelis et al. 2014), which makes the recovery of this component very difficult, even after the reintroduction of management (i.e., disturbances). Grasslands where disturbances have been excluded are also more likely to be invaded by exotic woody species, mainly *Pinus* spp. Management exclusion may occur in protected areas: the consequence is standing dead biomass accumulation, herbaceous diversity loss, shrub (and sometimes tree) encroachment (see Müller et al. 2023, Chap. 16, and Overbeck et al. 2023, Chap. 17, this volume, for more details).

If excluding endogenous disturbances has negative effects on grassland biodiversity and structure, excess of disturbances (intensity and/or frequency) are also problematic. Overgrazing increases erosion, decreases forage quality and quantity, decreases species diversity, and can provide opportunities for the invasion of the African grass *Eragrostis plana* Nees (Overbeck et al. 2007, Vélez-Martin et al. 2015), an extremely problematic species in the region (Guido et al. 2016). It has been estimated that, in 2008, *E. plana* already occupied 2.2 million hectares of grasslands in Rio Grande do Sul (Medeiros and Focht 2007). Similarly, a high frequency of fire may favor the spread of the alien legume shrub *Ulex europaeus* L. (Cordero et al. 2016). Other problematic invasive species in *Campos Sulinos* grasslands include the grasses *Cynodon dactylon* (L.) Pers. and *Urochloa* spp., the Asteraceae *Senecio madagascariensis* Poir., and species of the genus *Pinus* (see also Guido et al. 2023, Chap. 19, this volume). Moreover, wild boar (*Sus scrofa* L.) invasions have been reported for the *Campos Sulinos* region (Sordi and Lewgoy 2017). Initial research indicates severe impacts on vegetation, primarily because wild boar overturns the soil in the areas to feed on belowground plant organs, fungi, and invertebrates.

Beyond inappropriate management and alien species invasion, habitat conversion is the main threat to *Campos Sulinos* grasslands. Circa 60% of the original grassland cover has already been lost, mainly to agriculture and forestry (Vélez-Martin et al. 2015, Oliveira et al. 2017). Only in the Pampa, that is, the southern portion of the *Campos Sulinos* region, 38% of the original grassland cover was lost between 1985 and 2021 (reduction from 9.3 million hectares to 5.8 million hectares), while the agricultural area almost doubled (increased from 3.8 million hectares to 7.3 million hectares) (MapBiomas v7.0 2022). During the same period, the area with monocultures of exotic trees in the Pampa increased 17-fold from 1985 to 2021 (from 42,000 to 744,000 hectares; MapBiomas v7.0 2022), aggravating, in the case of *Pinus*, the problem of biological invasions. Land conversion leads to fragmentation and habitat area loss and thus negatively affects the biodiversity of grassland remnants, for example, by biotic homogenization (Staude et al. 2018). When converted areas are later abandoned, secondary grasslands may develop that considerably differ from primary grasslands, that is, grasslands that had never been subjected to land conversion (Koch et al. 2016; Leidinger et al. 2017; Torchelsen et al. 2019). In these cases, active restoration is necessary.

20.3 Demands and Requirements for Restoration

The continuous loss of grassland areas, principally in the recent years, is emblematic for the historical bias of conservation on forests (Overbeck et al. 2013), aggravated, in the case of the *Campos Sulinos* region, by low protection levels considering the extent of protected areas (see Overbeck et al. 2023, Chap. 17, this volume). A somewhat better consideration of grassland ecosystems in Brazilian environmental law is recent: with the Law for the Protection of Native Vegetation (*Lei de Proteção da Vegetação Nativa*, Brasil 12.651/12), in 2012, the consideration of non-forest ecosystems becomes more explicit (Menezes et al. 2021, Porto et al. 2021). This law includes two legal requirements that can significantly impact the demand for restoration: the Legal Reserve (RL, *Reserva Legal* in Portuguese) and the Areas of Permanent Protection (APP, *Área de Preservação Permanente* in Portuguese), that correspond to portions of each private property that must be conserved or restored (Metzger et al. 2019). APPs are to protect riparian corridors, steep slopes, and other sensitive ecosystems; their extent in the landscape thus varies according to geomorphology. The RL constitutes a fixed percentage, in the *Campos Sulinos* region 20% of the property, that is to be maintained with native vegetation cover but can be economically exploited in a sustainable way. Exemptions are made for landowners who converted areas for other uses before 2008. Private landowners whose property is not in accordance with these legal requirements, that is, who have a deficit in RL or APP, need to restore these areas. Despite the potential for significant restoration demands across all Brazilian biomes (Metzger et al. 2019), the implementation of the law poses challenges. Particularly in RS, the state that includes a substantial portion of the *Campos Sulinos* region, there are initiatives – without any scientific bases – to exempt grasslands that have been used as rangelands from the RL requirements (see details in Overbeck et al. 2023, Chap. 17, this volume).

Just as the conservation of grasslands in the *Campos Sulinos* region (for which a lack of specific protection requirements has been diagnosed; Porto et al. 2021; Rolim et al. 2022), the restoration of grasslands has received little specific attention until today. The national Environmental Regularization Program (PRA, *Programa de Regularização Ambiental* in Portuguese) aims to restore degraded areas in rural properties, specifically in RLs and APPs areas, that had been illegally converted (Brasil, 12.651/2012). However, this program has not yet been properly implemented by the governments of the South Brazilian states. Only recently some large restoration projects have been initiated, mostly due to specific calls of the Brazilian Biodiversity Fund (*Fundo Brasileiro para a Biodiversidade*, FUNBIO). While this needs to be applauded, limited current knowledge of restoration techniques (see below) may impede full restoration. By implementing the PRA and by reaching other restoration goals, such as those of the PLANAVEG, incentives to create a commercial demand might boost the development of an economic chain of ecological restoration, which is currently incipient in the *Campos Sulinos* region.

20.4 Restoration Strategies and Techniques of *Campos Sulinos* Grasslands

20.4.1 Degradation States and Restoration Strategies

As discussed above, the choice of the restoration strategy and, subsequently, of the most appropriate techniques for restoration will always depend on the degradation state of the site in question (e.g., see Guarino et al. 2023). In general, the more severe degradation, the higher the efforts necessary for restoration, and the longer restoration may take. However, the level of degradation is not always easy to assess, and first impressions may be deceiving. For example, a grassland invaded by alien grasses may at first glance appear closer to a native grassland than a site that until recently has been used as a tree plantation and, after cutting of trees, is devoid of vegetation. However, invasive alien species likely provide an even bigger limitation to restoration than trunk debris and leaf or needle litter layer that challenge grassland restoration after the use with silviculture (Porto et al. 2022). Few studies have been conducted comparing different conservation/degradation states of grassland in the region (Koch et al. 2016, Leidinger et al. 2017). Based on these studies, we can classify degraded sites into two main groups: those where changes in biodiversity and ecosystem properties are related to changes in management regime (i.e., without conversion of grassland vegetation), and those that were affected by land use change, which usually means more severe degradation (Fig. 20.1). However, invasive alien species may become dominant in both situations, which means that case-by-case evaluations are necessary. Figure 20.1 presents general patterns of changes in abiotic and biotic variables because of different types of degradation (i.e., positive, negative, or neutral effects) observed in *Campos Sulinos* grasslands. The

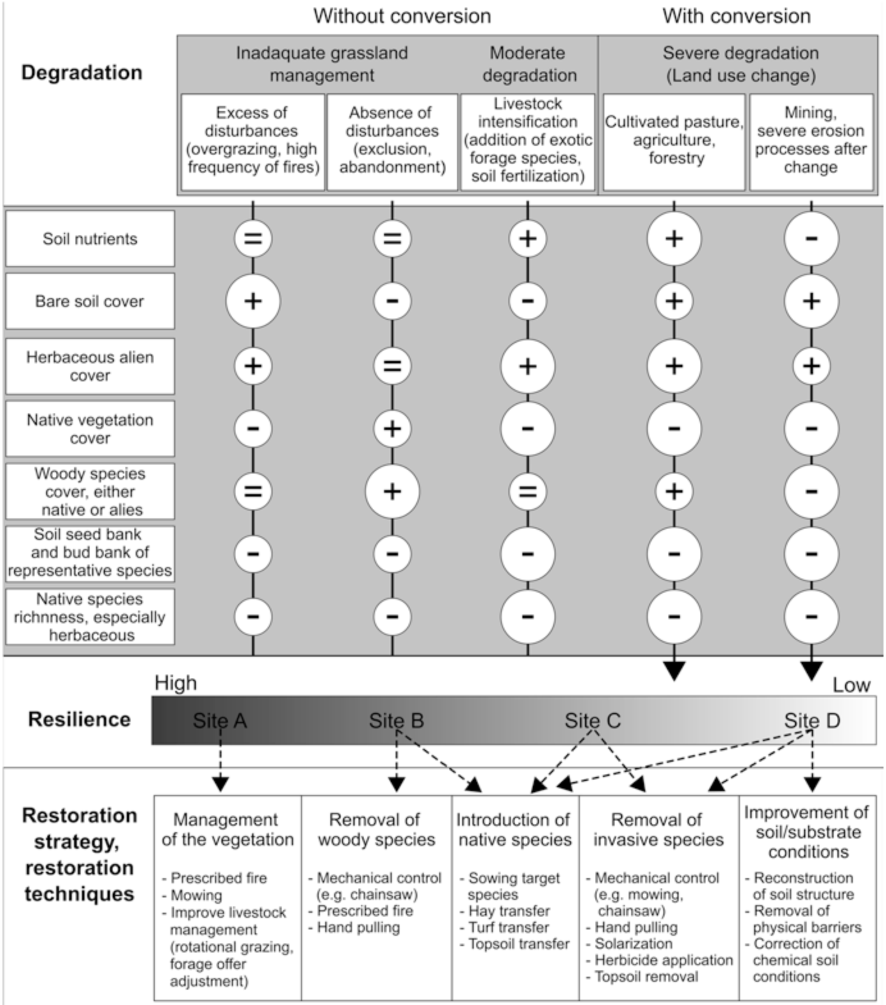

Fig. 20.1 Schematic representation of degradation effects on grassland properties that further influence ecosystem resilience and subsequent restoration strategies. Symbols (−) and (+) in the circles indicate the general pattern of how degradation influences the abiotic and biotic ecosystem properties. The symbol (=) indicates no or very little effect. The size of the circle indicates the magnitude or strength of the influence. (Sources: Baggio et al. 2018; Bonilha et al. 2017; Ferreira et al. 2020; Fidelis et al. 2014; Koch et al. 2016; Leidinger et al. 2017; Pañella et al. 2022; Porto et al. 2022; Silva and Fontana 2020; Sühs et al. 2020; Torchelsen et al. 2019; Vieira et al. 2015; Vieira and Overbeck 2020)

magnitude of these changes can vary due to historic features such as intensity and extent of the degradation process, the grassland ecosystem type, and region, as well as interactions with local environmental conditions. For instance, grasslands in the western portion of RS are more susceptible to degradation by overgrazing than highland grasslands in the northern part of the state because of higher evapotranspiration and more severe drought events in the region.

20.4.2 Restoration of Grasslands Degraded by Inadequate Management

When degradation is due to changes in the disturbance regimes (i.e., grazing and fire), abiotic and biotic shifts in the grasslands usually are less intense than at sites with a history of land conversion (Koch et al. 2016; Leidinger et al. 2017). If invasive species are absent, the reintroduction or adjustment of grassland management often is sufficient to recover typical structure and biodiversity (Fig. 20.2a). Removal of the accumulated biomass and of the woody species is a key step for restoration in these situations; whether this should best be done by fire, grazing, or mowing (Fig. 20.2b, c), or even by a combination of these techniques, depends on the specific situation as well as on the socioeconomic context (e.g., availability of domestic grazing animals or mowing machinery). After an initial reduction of biomass, regular management needs to be maintained to achieve grassland restoration targets. However, there may be situations where species introduction is necessary due to the low resilience of most herbaceous species. The diversity of typical grassland species may remain low even after reintroduction of management, as found, for the highland grasslands in RS state, after two decades of abandonment (Thomas et al. 2019a). The reason for this is the commonly low dispersal capacity and the reduction of the bud bank in the soil after long periods without disturbance (Fidelis et al. 2014). The use of fire as a restoration tool could be interesting, however, has not been studied so far in *Campos Sulinos* grasslands in sites excluded from management (but see Porto et al. 2022); care must be taken to not favor invasive species that respond positively to burns, such as gorse (*Ulex europaeus*; Cordero et al. 2016; Matthews 2005). When degradation is due to overgrazing, the reduction of grazing pressure may already improve the situation. Strategies such as deferred grazing (Fedrigo et al. 2018) or rotational grazing (Boavista et al. 2019) contribute to the fast recovery processes of vegetation. These strategies, easily applicable by landowners, also lead to increased productivity, which is important in the case of privately owned grasslands under grazing (Jaurena et al. 2021).

20.4.3 Restoration of Invaded Grasslands

Invasive species are a major problem throughout the *Campos Sulinos* region (see Guido et al. 2023, Chap. 19, this volume). Successful cases of true restoration of grasslands degraded by exotic species are still unavailable for the *Campos Sulinos* region, and research has been surprisingly little, given the magnitude of the problem. Studies to control the most problematic invasive species, African love grass

Fig. 20.2 Different techniques to restore *Campos Sulinos* grasslands that are currently under evaluation in scientific studies: (**a**) cattle management in degraded areas to restore vegetation structure and diversity; (**b**) mechanized mowing to remove excess of biomass and (**c**) manual mowing of abandoned grassland, both to improve light incidence and resprouting; (**d**) tree logs placed over bare soil are not a restoration technique, but serve as inspiration to develop techniques to increase seed rain and improve site conditions; (**e**) mechanized chemical control of invasive grasses, such as *Eragrostis plana*; (**f**) topsoil removal to control invasive grasses; (**g**) manual herbicide application to control invasive species, such as *Urochloa decumbens*; (**h**) mechanized seed harvest on donor grasslands to obtain seeds of native species to use for restoration, (**i**) hay transfer in an experimental plot. (Photos: (**a**) Marcelo Mentges; (**b**) Rodrigo Dutra-Silva; (**c**, **d**, **f**, **h**) Pedro Augusto Thomas; (**e**) Projeto Pró-APA Sustentável; (**g**) Lua D. Cezimbra; (**i**) Ana Boeira Porto)

E. plana, are not new (see Coelho 1985). However, historically these studies aimed at controlling the invader to create productive grasslands for livestock raising, using herbicide application and sowing exotic forage species (e.g.,: Gonzaga and Gonçalves 1999; Perez 2015; Reis et al. 2008), but did not aim at recovery of the native plant community. Despite the advances regarding knowledge of ways to control the invasive species these approaches bring, they cannot be considered to be ecological restoration, because native ecosystems were not a target.

Studies aiming to evaluate techniques to restore native grassland invaded by *E. plana* have been developed from the 2010s on. In lightly invaded areas, adequate grazing management can limit the cover and expansion of *E. plana* (Baggio et al. 2018). Importantly, open soil needs to be avoided, even in lightly invaded areas, as it promotes the establishment and growth of the species (Baggio et al. 2018). In moderately invaded areas, hand-pulling, clipping, or herbicide can reduce *E. plana* cover; however, removal of the invader was not sufficient for plant species composition to become similar to that of non-invaded communities (Guido and Pillar 2017). Studies that actively aim to recover plant community composition in grasslands invaded by other species are scarce. Thomas et al. (2019b), working in grasslands dominated by *Urochloa decumbens* (Stapf) R. Webster, had an initial success in controlling the invader through chemical (Fig. 20.2g) and topsoil removal (Fig. 20.2f), but did not manage to improve community composition of the grassland. Long-term management actions appear to be necessary to achieve a species composition similar to that of reference grasslands. Chemical control (Fig. 20.2e, f) may not be the best option of choice, because it not always leads to increased similarity of degraded sites with reference sites in terms of community composition (Guido and Pillar 2017). Topsoil removal also is not a useful tool over large areas, due to high costs and the potentially negative effect on native species still in the invaded community. Recently, studies are underway testing the use of plastic tarps to control *U. decumbens*, apparently with some success (L. D. Cezimbra & G.E. Overbeck, unpublished results; see Box 20.1 for more details).

Among woody invaders, gorse (*U. europaeus*) and pine (*Pinus* spp.) are the most problematic species for the grasslands in the region (see Guido et al. 2023, Chap. 19, this volume). Porto et al. (2022) conducted experiments to restore coastal grasslands degraded by former use for pine plantation. They evaluated different methods to remove the dense layer of pine needles (by controlled burns and mechanical removal) and the efficiency of seed introduction by hay transfer. The removal of the needle layer is a necessary first step in the restoration of grasslands as it impedes the recovery of the vegetation. Due to the higher cost of mechanical removal, controlled burns should be the option that is more feasible for larger areas. Moreover, the application of fire also led to the destruction of pine seeds found in the area: in the mechanical removal treatment, the emergence of pine trees was significantly higher, which presents a considerable obstacle to the restoration of these sites (Porto et al. 2022). This is indicative of fire as a potentially interesting tool to control pine invasion in grasslands.

Independent if invasive species are herbs, shrubs, or trees, in most cases, steps beyond the control and eradication of the invasive species itself are necessary for ecological restoration. The reason is that invasive species generally reduce native plant diversity by their high abundance (e.g., Cezimbra et al. 2021, Guido and Pillar 2017, Thomas et al. 2019b), or due to shading and litter production, as in the case of trees such as pine. Spontaneous recovery of native plant populations often is slow or does not occur at all, and active introduction of plant species is necessary, discussed in the next topic.

20.4.4 Restoration of Sites with a History of Land Conversion

As described above, *Campos Sulinos* grasslands have low resilience to exogenous disturbances. Diversity of native plants usually is considerably reduced in areas under passive restoration after periods of land use with agriculture (old fields) or forestry (Koch et al. 2016; Bonilha et al. 2017; Torchelsen et al. 2020). The plant communities of secondary grasslands differ from their counterparts in primary reference grasslands, often due to the presence of exotic species. Many species that are common in reference grasslands are likely limited in terms of dispersion and establishment success. It has been shown that the soil seed bank even in well-conserved sites does not include the most typical species of the established plant community (Minervini-Silva and Overbeck 2020), which reduces their capacity for natural regeneration by seeds from the soil bank. Natural regeneration from seeds after habitat conversion is even less effective (Vieira et al. 2015; Vieira and Overbeck 2020). For *Campos Sulinos* grasslands, resprouting from belowground bud banks is crucial for the maintenance of plant populations and thus communities crucial (see Fidelis et al. 2014). This means that any process that led to the complete removal of the original grassland vegetation cover is problematic for post-disturbance vegetation recovery. In situations of severe degradation, it is necessary to actively introduce native species. While this still is one of the biggest challenges for grassland ecological restoration in the region, recent studies have contributed to overcome this barrier (Table 20.1, Fig. 20.2). In the following, we give an overview of the current state of knowledge of species introduction in *Campos Sulinos* grasslands.

Direct sowing is a well-established technique to restore temperate grasslands in the Northern Hemisphere (Kiehl et al. 2014; Shaw et al. 2020). At current, in the *Campos Sulinos* region, only two native species are sold as seeds (*Axonopus affinis* Chase and *Axonopus compressus* (Sw.) P. Beauv.), primarily for use in gardening (Rolim et al. 2022). Besides these species, seeds of a cultivar (regionally called *pensacola*) of the native *Paspalum notatum* Flüggé, which is highly abundant in grazed grasslands, are available for use as forage species. However, the use of cultivars is generally not recommended for ecological restoration due to risks for genetic diversity (Aubry et al. 2005), failure in successfully achieving a desirable native plant community (Nevill et al. 2016), and seeds not-adapted to harsh local conditions commonly found in degraded sites (e.g., Thomas et al. 2019b). Thomas et al. (2019b) tested direct sowing of 6 g/m^2 of a low diversity mix (three grass species), using cultivated grasses, but establishment success was extremely low. This was likely a consequence of harsh site conditions; possibly native species, better adapted to these conditions, would have performed better. However, seeds of native wild species are inexistent on the restoration market in South Brazil, which constitutes an immense constraint for ecological restoration in the region. Furthermore, the incipient knowledge about the germination and establishment from seeds of native species also complicates attempts to work with seeds collected manually in the field (see Guarino et al. 2018): currently, the risk of failure is high. Clearly, the low availability of native seeds limits the restoration of grasslands in the *Campos Sulinos* region (Dutra-Silva 2023), where, frequently, more than 20 species can be found in one square meter of grasslands, often much more (Menezes et al. 2022).

In response to the lack of seeds on the commercial market, researchers have focused on alternative ways to introduce species in grassland restoration. One interesting approach in this context is the mechanized harvesting of seeds in conserved areas by the use of brush harvesters. Relatively simple machines for this have been

Table 20.1 Overview of studies that assessed restoration techniques efficiency on vegetation in *Campos Sulinos*

Objective	Technique	Main results
Species introduction	Direct sowing	Mix with *Paspalum notatum*, *P. guenoarum,* and *Axonopus affinis* without success (Thomas et al. 2019b)
	Hay transfer	Contrasting results, indicating that the technique has potential, but needs to be further studied (Porto et al. 2022; Thomas et al. 2019a, b; Vieira 2018)
Invasive grass control	Topsoil removal	Success in controlling *U. decumbens* (Thomas et al. 2019b)
	Herbicide	Success in controlling *U. decumbens* (Thomas et al. 2019b) and *E. plana* (Guido and Pillar 2017)
	Manual removing	Success in controlling *E. plana* with hand-pulling and clipping the aboveground biomass (Guido and Pillar 2017)
Improved site conditions	Prescribed fire	Contrasting results in studies aiming to remove the pine needle layer on the soil and to control pine establishment: positive results in coastal grasslands (Porto et al. 2022), and inefficient in highland grasslands (Vieira 2018)
Vegetation management	Grazing and mowing	Mowing and grazing were efficient to control shrubs and promote plant diversity; but not to control *E. plana* (Dutra-Silva et al. 2022)
	Mowing	Few mowing events (2 or 3) over short periods (less than 9 months) increase plant diversity in a grassland without disturbance for 20 years (Thomas et al. 2019a)
	Deferment and rotational grazing	Short temporal exclusions of cattle in overgrazed areas allow the vegetation to recover (Fedrigo et al. 2018). Rotation grazing increased plant biomass and plant diversity (Boavista et al. 2019).
Seed traps	Tree logs	Tree logs placed over bare soil served as seed traps and increased the establishment of wind-dispersed grassland species (Porto et al. 2023)

previously used in grasslands in Uruguay and Argentina (Machín 2017; Siota et al. 2021). Recently, a similar harvesting equipment was developed in Rio Grande do Sul and is currently under evaluation in pilot projects (Fig. 20.2h). As such machines collect a wide range of mature seeds available in donor grasslands at the moment of harvesting, chances of establishment success are higher: we can expect at least some species to show establishment success at degraded sites.

Another alternative to introduce species is through hay transfer (Fig. 20.2i). This technique aims to introduce species by spreading aboveground biomass that was cut in a well-conserved grassland at a moment when many species present mature seeds (i.e., hay with seeds) over a degraded area. Easy to replicate, low-cost, and successfully employed to restore temperate grasslands in Europe (Kiehl et al. 2010), this technique has been tested in several restoration experiments in the *Campos Sulinos* region (Table 20.1). The studies tested single applications of 500–750 g/m^2 of hay collected once (except for Vieira 2018, who combined two hay harvests). The different studies show a great variation in the success rate in terms of increase plant cover and plant species richness. In the studies of Vieira (2018) and Porto et al.

(2022), hay transfer was an efficient technique to introduce native species and increase plant cover in former pine plantations. On the other hand, hay transfer applied by Thomas et al. (2019a, b) did not had the same efficiency in an experimental restoration of an old field invaded by *U. decumbens* and a grassland without management for a long time, respectively. This points out that applicability of the method can vary according to the specific situation where hay is being used or collected. For instance, hay collected in late summer showed low efficiency in some cases (Thomas et al. 2019b) and good results in others (Vieira 2018, Porto et al. 2022). Specific site conditions, climatic variation, and hay-donor site characteristics may influence the result, just as they should define the ideal amount of hay to be used and when to harvest it. Clearly, results from single studies cannot be easily generalized. Studies at larger scales and under distinct conditions are necessary to better understand the applicability of hay transfer to restore *Campos Sulinos* grasslands.

Independent of how seeds are introduced, it is also important to consider the necessity to improve local site conditions (e.g., Bischoff et al. 2018; Goret et al. 2021; Shaw et al. 2020). Harsh soil conditions (Thomas et al. 2019b) or longer drought periods may lead to failures in the germination and establishment of introduced species. Improving physical conditions and water availability in the initial restoration phases are actions that obviously require considerable resources, however, may be necessary to avoid failure of restoration. When no elaborate techniques are available, creativity may help: ‘unintentional’ experimentation with tree logs that appear to have both improved microsite conditions and increased seed rain (Fig. 20.2d, see Porto et al. 2023) may serve as inspiration.

Finally, cattle also can be actively used to transport seeds when transferred from sites with large amounts of ripe seeds of target species to degraded sites. Minervini-Silva and Overbeck (2021) showed that large numbers of seeds and species are transported in the feces of domestic cattle, and these seeds can potentially contribute to vegetation development. This alternative should be tested in field conditions; if successful, the use of cattle as a restoration agent could change the game of grassland restoration in private properties, as these grasslands are under livestock grazing which should facilitate restoration.

20.5 Current Limitations to Grassland Restoration in the *Campos Sulinos* Region

20.5.1 Species Introduction

The introduction of native species remains a challenge in *Campos Sulinos* grasslands and more studies should be developed. Other techniques than the once mentioned earlier, for instance, transplantation of turfs, topsoil, and seedlings, have not yet been tested. We also need to improve our knowledge about germination and establishment of native species, used separately or in mixes. Lists of species that are potentially interesting for use in restoration projects have already been proposed (see Guarino et al. 2018). However, for the majority of species listed, no information regarding strategies for seed collection, optimum storage conditions, germination rate, dormancy breaking requirements, and establishment rate are available, thus limiting their use in real-life restoration beyond experimental plots. Clearly, the lack of seed material is a key constraint for the restoration of grasslands in the *Campos Sulinos* region.

20.5.2 Scale

The majority of the studies listed in Table 20.1 were developed as scientific experiments, in small plots or small areas (<100 m^2) and over short periods (mean duration of studies: 2 years). Besides the unquestionable value of such studies, generalizations about the potential of these techniques to contribute to restoration in larger areas should be made with caution. Similarity to the reference system is not rapidly achieved by active restoration in general (Holl and Aide 2011); in the case of the *Campos Sulinos*, the high taxonomic and functional diversity of natural grasslands may turn restoration processes even more time-demanding. A considerable portion of plant species diversity in the *Campos Sulinos* is composed of slow-growing forbs that show a low ability for seedling recruitment and colonization (Overbeck and Müller 2018). Thus, time is an important component to reach ecological restoration success, which will need to be considered in research projects and pilot studies as well. In addition, restoration should always consider the landscape context which can be decisive for the potential of natural recovery (Holl and Aide 2011), but also for the risk of alien species invasions. Experimental plots are limited in this regard.

20.5.3 Fauna

Effectively restored ecosystems obviously consist of more than plants which constitute the component of the ecosystem that often is the main focus of restorationists. So far, consideration of the fauna in the restoration of *Campos Sulinos* grasslands has been very timid, both as restoration target and in monitoring. To the best of our knowledge, only two studies that monitor the effect of restoration, or recovery, of degraded grasslands are available. Bird species richness and abundance showed a rapid recovery in a comparison of secondary grasslands under active restoration with native grasslands (Silva and Fontana 2020). In contrast, ant communities showed lower species diversity and different compositions when comparing secondary grassland that recovered without active restoration interventions to primary grasslands under grazing (Dröse et al. 2021).

20.5.4 Social and Economic Aspects of Restoration

There is clear evidence that livestock grazing is compatible with the conservation and restoration of *Campos Sulinos* grasslands. This offers the potential to integrate restoration into productive land management on private properties in a region where cattle ranching is a key economic activity: ecological restoration may improve productivity of grasslands. However, financial incentives are necessary to stimulate restoration, as restoration per se is not a priority to landowners (Henderson et al. 2016). At any rate, the development of a restoration market will mean job opportunities and income for human populations and thus improve conditions of life. In Brazil, experiences exist with the creation of networks for the collection of native seeds for ecological restoration in the Cerrado, Amazon, and Atlantic Forest regions (Urzedo et al. 2022). A key element to the success of these experiences is the existence of a demand for seeds from restoration. The implementation of restoration activities, also in response to a legal obligation (e.g., in the context of the PRA; see above), thus appears to be crucial to maintain these networks, or establish new ones, for example in the *Campos Sulinos* region. Restoration of degraded areas in public lands may be a crucial first step towards the development of restoration markets as these areas that are already under the responsibility of public agencies and thus could be immediately restored (Dutra-Silva 2023). Volunteers also may have an important role in restoration and invasive species control programs, especially in small protected areas (see Dechoum et al. 2019). In addition, projects that stimulate or enhance the participation of local communities in restoration are helpful as they create interest for restoration and illustrate restoration benefits (see Box 20.2). However, at present, these potentials are still far from being used to advance restoration.

20.6 Necessary Steps to Advance in Restoration of the *Campos Sulinos*

The sections above clearly indicate that restoration of grasslands in Southern Brazil is at its very beginning. No consolidated techniques to restore grasslands after more severe degradation exist for the region, even though we are well into the UN Decade of Ecosystem Restoration. The inexistence of seeds of native species on the market is a severe limitation for all restoration activities at the moment: clearly, this is a key issue to be addressed in research, but also creating the necessary institutional framework, which is still not well developed. In the following, we summarize key issues that need to be addressed to be able to really tackle the ecological restoration of the *Campos Sulinos*.

20.6.1 Raising Awareness and Implementing Priority Actions for Restoration

Advances in ecological restoration do not only depend on knowledge of appropriate techniques and available seeds but, principally, on awareness on the need of restoration and of the important benefits it brings not only to biodiversity but also to society. At present, this awareness is still very low in the *Campos Sulinos* (Porto et al. 2021), which also reflects in slow progress regarding the implementation of restoration activities that are necessary to reach objectives of government strategies, e.g., of Brazil's PLANAVEG. The following actions are necessary:

- Recognition and valorization of the ecological, cultural, and economic importance of the *Campos Sulinos*;
- Implementation of existing governmental programs (such as PRA) for the restoration of grasslands on private land;
- Development of programs to restore degraded areas on public land, mainly in protected areas;
- Development of economic incentives and valorization of products from native grasslands, stimulating conservation and restoration of grasslands;
- Support of land use practices compatible with the biological characteristics of *Campos Sulinos* grasslands, such as traditional grazing.

20.6.2 Advance in Terms of Technical and Scientific Knowledge

All restoration actions should be based on the best scientific information available. Given the lack of knowledge on which restoration activities are the most suitable for specific conditions and especially given the lack of information on seed-based restoration, strengthening research on the field clearly is a key to improve restoration. In this context, the following steps are important:

- Development of research activities in different areas of the field of restoration ecology (including restoration techniques, techniques of plant propagation restoration management, restoration monitoring, and social and economic drivers of restoration, among others) to provide conceptual and technical bases for ecological restoration;
- Definition of priority species to be used in restoration, based on clear criteria;
- Development and implementation of monitoring protocols and evaluation of restoration success over a large range of projects;
- Development of reliable cost estimates for grassland restoration in different scenarios;
- Sharing of scientific knowledge on restoration and grassland management beyond academic institutions.

20.6.3 Ecological Restoration in Practice

Restoration in practice needs more than scientific underpinning. In order to work, adequate infrastructure and financing of the restoration sector are necessary and ecological restoration needs to be strengthened considering several aspects:

- Support the development of supply chains relevant to restoration, especially regarding seeds and seedlings;
- Empowerment of local communities, landowners, and stakeholders to become engaged in the restoration process;
- Stimulation of the creation of associations and networks, for example for seed collection;
- Dissemination of successful restoration activities to society.

In the *Campos Sulinos* region, concentrated efforts are necessary to reach the ambitious restoration goals set by PLANAVEG or in international agreements. Even though our knowledge of how to restore grasslands is incipient in many aspects, restoration actions need to be multiplied quickly. This means that researchers, restoration practitioners, and decision-makers need to collaborate to implement ecological

Box 20.1: Testing Plastic Tarts to Control an Invasive Grass in a Protected Area

The restoration of areas degraded by invasive grasses still lack efficient protocols, both concerning control of the invasive species and recovery of the native plant community. Protected areas can be considered priority areas for restoration. An interesting example is a project on the control of *Urochloa decumbens* in the Banhado dos Pachecos Wildlife Refuge, Viamão, RS, Brazil. Motivated by the advance of the invasive grass over the habitat of two endangered animal species (the rodent *Ctenomys lami*, and the ground-nesting bird *Hydropsalis anomala*), the objective was to test alternative techniques to herbicide application to control an invasive grass, using solarization with the help of plastic tarts. The use of tarts for weed control and elimination of other microorganisms is commonly employed in horticulture. In an experimental approach, the effect of black and transparent sheets (Fig. 20.3a) with different lengths of application (30 and 60 days) was evaluated and compared with the effectiveness of herbicide application. Initial results (Fig. 20.3b) show that multiple applications of the plastic sheets are necessary to eliminate individuals of the invasive species that reestablishes from the soil seed bank once the tarps are removed. While a return of native vegetation has been observed in areas adjacent to uninvaded native grasslands, it is still unknown which species are capable of occupying the site once *U. decumbens* is controlled. In the meantime, the park manager has successfully implemented restoration

(continued)

Box 20.1: Continued

activities over a larger area and with tougher sheets. Future research should monitor vegetation development and, if necessary, develop efficient ways of seed introduction.

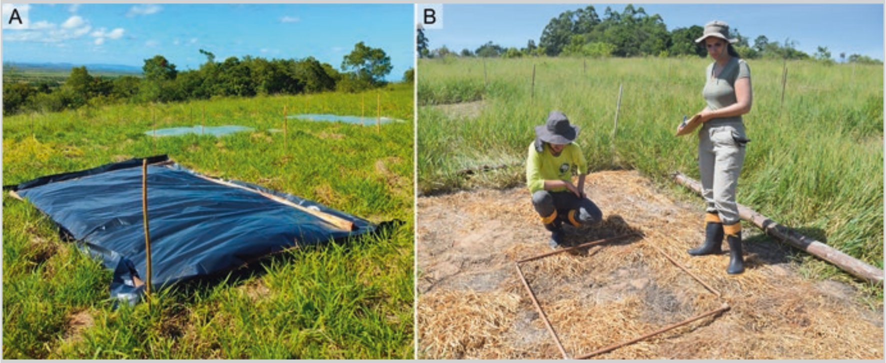

Fig. 20.3 Experiment with plastic tarts to control *Urochloa decumbens* and restore natural grasslands in Banhado dos Pachecos Wildlife Refuge, Viamão, Brazil. (**a**) Black and transparent plastic tarts (front) and transparent (back); (**b**) researchers evaluating treatment effects after removal of the plastic sheets. (Photos: (**a**) Lua D. Cezimbra; (**b**) Luiz Felipe Fonseca da Rocha)

Box 20.2: Integrating Local Communities in Ecological Restoration Projects

The participation of local communities in restoration projects not only increases acceptance but may even lead to the development of economic opportunities. An example is provided by a project on restoration by *Butia* palm groves (Fig. 20.4a) led by the Brazilian Agricultural Research Corporation EMBRAPA. The objectives of the project '*Rota dos Butiazais: fortalecimento da cadeia produtiva do butiá associada à recuperação da vegetação nativa na região do Parque Estadual do Podocarpus (Encruzilhada do Sul, RS)*' go beyond the restoration of the plant community. It also aims at the strengthening of the productive chain of products derived from the palm *Butia* sp. The project is developed in the region of Podocarpus State Park, in Encruzilhada do Sul, RS, Brazil; a region that has seen strong land use change and where palm groves dominated by *Butia capitata* are typical ecosystems. Alongside active restoration activities, such as transplantation of *Butia* individuals who were at risk and experimentation on grassland restoration, the project also included workshops for the local community (rural producers, local students, teachers, and school cooks) to improve the knowledge of grassland ecology, as well as stimulate interest on the restoration of

(continued)

Box 20.2: Continued

ecosystems and the sustainable use of the native palm. A culinary workshop, offered to cooks from schools in the region, presented recipes with *Butia* sp., such as cakes and jams, who could gain weight in the local community. A workshop on plant arrangements using native grasses with ornamental potential aimed to change the perspective on natural grassland vegetation in the region by highlighting the potential for the use of native species. Other workshops conducted for the local community presented concepts and techniques of restoration ecology as well as bases for the recognition of native species (Fig. 20.4b). These workshops were important to stimulate the interest of local people in native plants and ecosystems of the region and raised awareness for conservation and maintenance of natural resources.

Fig. 20.4 Photos from workshops conducted within the project in Encruzilhada do Sul, RS, Brazil. (**a**) *Butia* sp. palm trees associated with grasslands; (**b**) workshop presenting the concepts and techniques of restoration ecology. (Photos: (**a**) Rosa Lía Barbieri; (**b**) Arthur Lenzi da Silva)

restoration and at the same time develop it further. Ecological restoration is a key for the future of the *Campos Sulinos*, and this deserves high efforts from society.

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