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Disrupting a socio-ecological system: could traditional ecological knowledge be the key to preserving the Araucaria Forest in Brazil under climate change?

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Abstract
Socio-ecologicalsystems (SESs) hinge on human groups and ecosystems, promoting interdependence and resilience to environmental disturbances. Climate change effects propagate from organism to biomes, likely influencing SES. In southern and relict patches in southeastern Brazil, Araucaria Forest is a typical SES due to the historical interaction between humans and biodiversity. We thus aimed to evaluate empirically and theoretically how climate change could disrupt this system by interviewing 97 smallholders and assessing their traditional ecological knowledge (TEK). We evaluated and measured the following: (i) socioeconomic impact of araucaria's nut-like seed (*pinhão*) trade; (ii) ethnoecological knowledge about climate change; and (iii) generated an ecosystem services network. We projected these empiric data with a projected loss of 50–70% of the Araucaria Forest due to climate change to quantify the risks of the potential disruption of this socioecological system. We found evidence that to avoid the disruption of the Araucaria Forests is paramount to value TEK holders, safeguard the historical socioecological interaction, and promote non-mutually exclusive measures in an integrative response to maintain the Araucaria Forests resilient to future disturbances.

Keywords Araucaria Forest system · Climate change · Ecosystem services network · Ethnoecology · Mixed ombrophilous forest · *Pinhão* management

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1 Introduction

Climate change effects have been widely described throughout all ecosystems (Malhi et al. 2020), from organism to biome levels (Parmesan 2006), affecting the genetics of organisms (e.g., allelic diversity) and the integrity of biomes, including their ecological resilience to disturbances (Bellard et al. 2012). These threats also impinge on socio-ecological systems (hereafter SESs), which consist of the integration of local human groups with ecosystems, promoting reciprocal feedbacks, interdependence, and resilience (Folke et al. 2010). These local human groups commonly rely on interactions with natural assets and are represented in Brazil by Indigenous Peoples, local communities (e.g., ribeirinhos, caiçaras), or even small landowners (De Souza et al. 2006; Fatorić and Chelleri 2012; Gomes et al. 2018; Tagliari et al. 2021a). These groups are characterized as holding traditional ecological knowledge (hereafter TEK): a long-term experience based on observation, use, and management of natural resources, from removal of non-useful plants, fire and soil management, selection of useful plants, among others, thus contributing to extensive modifications in ecosystems, from pristine forests to domesticated landscapes (Levis et al. 2017; Molnár and Babai 2021).

Ecosystems with continuous interactions between plants and peoples are examples of SESs. For instance, enduring human-plant interactions in the Neotropics contributed to enhancing plant domestication and food security across Amazonia (Levis et al. 2018) and the Araucaria Forest in southern Brazil (Cruz et al. 2020). The Araucaria Forest, also known as Araucaria Mixed Forest, is an emblematic SES in the subtropical Atlantic Forest region (Tagliari et al. 2021a). The main plant species in this ecosystem is *Araucaria angustifolia* (Bertol.) Kuntze, a conifer with a candelabra aspect that is popularly known as araucaria or Brazilian Pine, critically endangered according to the International Union for Conservation of Nature, because it was almost depleted by extensive and illegal logging in the early to late twentieth century (Thomas 2013). The species plays a key ecological role in the ecosystem's functioning due to its nut-like seed called *pinhão*. The nutritious *pinhão* structures the associated vertebrate consumers spatiotemporally (Oliveira-Filho et al. 2015; Bogoni et al. 2020a). The species has an ancient connection with Indigenous Peoples and local communities (Reis et al. 2014; Robinson et al. 2018) who still use and manage *pinhão* (Adan et al. 2016; Quinteiro et al. 2019). Forest management strategies used by human groups over the last 1400 years expanded the Araucaria Forest beyond its natural boundaries, and many of these landscape modifications are still visible (Robinson et al. 2018; Cruz et al. 2020).

Currently, the traditional araucaria management systems of local smallholders do the following: (i) maintain productive forest fragments (Mello and Peroni 2015); (ii) promote ecosystem services (Tagliari et al. 2019) and temporal food security for local fauna and human groups (Adan et al. 2016; Bogoni et al. 2020a); (iii) preserve cultural, social, and economic dynamics in this SES (Zechini et al. 2018; Tagliari et al. 2021a); and (iv) maintain the functional diversity of Brazilian Pine, especially due to the identification of *pinhão* ethnovarieties thanks to TEK holders (Adan et al. 2016; Tagliari and Peroni 2018; Quinteiro et al. 2019). These traditional systems managed by TEK holders also boost positive feedbacks that might expand the Araucaria Forest (Tagliari et al. 2021a). Consequently, Brazilian Pine is also classified as a "cultural keystone species" (Garibaldi and Turner 2004), since it plays cultural and socio-ecological roles in southern Brazil (Reis et al. 2014; Adan et al. 2016; Quinteiro et al. 2019). Both cultural and ecological keystone aspects of the Brazilian Pine reinforce the argument that the entire ecosystem behaves as a socio-ecological system (Tagliari et al. 2021a).

However, chronic deforestation, agricultural expansion, and, more recently, climate change (Orellana and Vanclay 2018; Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020) have been hindering Brazilian Pine conservation and the resilience of this SES. To halt biodiversity losses, the creation of protected areas is a cornerstone strategy (Geldmann et al. 2013). Araucaria Forest remnants are still poorly encompassed by the existing protected area network. Recent studies showed that less than 10% of the projected distribution of *A. angustifolia* falls within existing protected areas in present and future climate change scenarios (Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020; Tagliari et al. 2021b). From almost 1500 years before present (BP) until the late nineteenth century, the Araucaria Forest extent covered an estimated area of 200,000 km^2 that spanned parts of Brazil, Argentina, and Paraguay (Nodari 2016). Due to deforestation, no more than 30% of the Araucaria Forest remnants remain preserved (Rezende et al. 2018). Moreover, future climate change predictions indicate losses of climatically suitable areas ranging from 60 to 96.5% compared to the current distribution of the species (Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020).

Although these studies showed the vulnerability of the species to climate change, they all failed to properly identify what is at stake if climate change disrupts this SES, by their failure to examine potential losses in ecological, social, and economic aspects. Also, these studies do not consider the historical human-plant interactions and the possibilities they offer to increase resilience to anthropic disturbances (Tagliari et al. 2021a). We aimed to fill this knowledge gap by approaching one of the main actors behind the resilience of the Araucaria Forest SES, local smallholders. Doing this is important for three main reasons. First, they possess TEK related to Brazilian Pine use and management (Mello and Peroni 2015; Adan et al. 2016; Quinteiro et al. 2019). Second, Brazilian legislation has a specific protected area category for private property, *Reservas Legais* (legal reserves), which are compulsory protected areas that host almost one-third of all remaining native vegetation in the Atlantic Forest (Metzger et al. 2019), including Araucaria Forest fragments. Consequently, TEK holders preserve the majority of the native Brazilian Pine remnants because, in southern Brazil, 20% of the land on private properties must be retained as native vegetation (Orellana and Vanclay 2018). Third, communities of poor smallholder farmers might be one of the most vulnerable groups due to global environmental changes (Pyhälä et al. 2016) and, by looking at them in a social, economic, ecological, ethnoecological, and ecosystem perspective, they might be one of the major human groups contributing to the conservation of this ecosystem.

Thus, we examine the aspects within the Araucaria Forest SES that might be at risk due to climate change by looking at a social, economic, ecologic, ethnoecological, and ecosystem services framework. Furthermore, we describe how TEK holders could increase the Araucaria Forest's resilience to climate change. To achieve these objectives, we interviewed 97 smallholders throughout the Araucaria Forest. Based on an assessment of their TEK, we systematically describe why this specific human group might be critical to safeguarding the entire Araucaria Forest SES by maintaining its preservation, ecosystem services, Brazilian Pine functional diversity (intraspecific diversity), socio-ecological interactions, resilience to disturbances and, especially, by helping it avoid disruption by climate change.

2 Materials and methods

2.1 Study area

The study was conducted throughout the extent of the original distribution of the Araucaria Forest, where these interactions between human groups and *A. angustifolia* still occur (Fig. 1). Historically, the extent of the Araucaria Forest was distributed along highland plateaus at altitudes above 500 m (de Souza et al. 2009), especially in Brazil's Southern region (states of Paraná, Santa Catarina, and Rio Grande do Sul) and relict patches in the Southeastern region (states of São Paulo, Minas Gerais, and Rio de Janeiro) of Brazil (Quinteiro et al. 2019; Tagliari et al. 2021b).

2.2 Traditional ecological knowledge in the Araucaria Forest system in a nutshell

Different human groups have interacted with the Araucaria Forest over time. Use and management date back to pre-Columbian times, when paleo-Indigenous ethnic groups cultivated *pinhão* (the nut-like seed of Brazilian Pine) for subsistence or religious reasons (Reis et al. 2014). Their historical footprint changed the forest landscape; archaeological data indicate humans influenced the expansion of the forest in the past (Robinson et al. 2018; Cruz et al. 2020). Currently, human groups (i.e., Indigenous Peoples and local smallholders) still rely on Araucaria Forest resources, especially in relation to the use and management of *pinhão* and other plant species, such as *Ilex paraguariensis* (Aquifoliaceae family), known as *yerba-mate*, a tea-like beverage (Reis et al. 2014), and *Acca sellowiana* (Myrtaceae family), known as *goiabeira-serrana* (Bogoni et al. 2018).

This long-lasting interaction created productive forest management systems that promote "conservation-by-use" (Reis et al. 2018), as well as benefits to human groups, such as (i) economic (*pinhão* trade), (ii) social (cultural identification), (iii) subsistence (food security), and (iv) socio-ecological (environmental services, ecological resilience, and

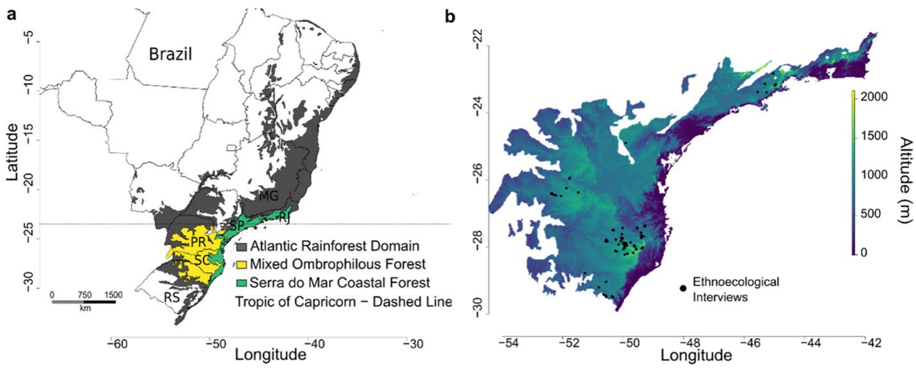

Fig. 1 **a** The Atlantic Forest (dark gray), Araucaria Forest ecoregion (yellow) — the three Brazilian states that mainly encompass this ecoregion: Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS). The Serra do Mar Coastal Forest (green) holds relict Araucaria Forest remnants, especially at Mantiqueira region along Minas Gerais (MG), São Paulo (SP), and Rio de Janeiro (RJ) borders. **b** Altitude map areas along the studied area; black dots represent the locations of the 97 ethnoecological interviews conducted in this study, from São Francisco de Paula (RS) to Cunha (SP)

functional diversity of *pinhão*) (Mello and Peroni 2015; Adan et al. 2016; Reis et al. 2018; Zechini et al. 2018; Quinteiro et al. 2019; Tagliari et al. 2021a). The functional diversity of *pinhão* (ethnovarieties) is well described in the literature as an example of TEK held by local smallholders (Adan et al. 2016; Tagliari and Peroni 2018; Quinteiro et al. 2019).

The identification of different ethnovarieties shows aspects of how intricate this human-plant relationship is, indicating food security spatiotemporally (Bogoni et al. 2020a), economic dependence (Adan et al. 2016; Quinteiro et al. 2019; Tagliari et al. 2021a), and knowledge about Brazilian Pine phenology, distribution, threats, uses, or management (Adan et al. 2016; Tagliari and Peroni 2018; Reis et al. 2018; Quinteiro et al. 2019; Bogoni et al. 2020a; Tagliari et al. 2021a). Thus, we requested for local smallholders and *pinhão* extractors their consent to answer a semi-structured questionnaire (Table S1), following the International Society of Ethnobiology (ISE) ethical norms. We used the snowball technique to find participants for the semi-structured interviews. This method searches new potential participants indicated by previous participants in each semi-structures interview. Sampling sufficiency occurs when a nominee has already been interviewed in the region (Bernard 2006). We aimed to include Indigenous Peoples as TEK holders, such as the Southern-Jê and Guarani groups, who have shaped forests composition in southern Brazil (Cruz et al. 2020); however, ethical limitations and legal aspects prohibited us from including them in our study. Our research was approved by the ethics committee at the Universidade Federal de Santa Catarina (CAEE: 86,394,518.0.0000.0121), following the code of ethics of ISE.

2.3 Socioeconomic data

We defined two distinct strategies to compile socioeconomic data. First, leaning on our semi-structured interviews, we collected information about the interviewees: gender, age, profession, main crops cultivated, time living on the property, how much the *pinhão* trade boosts family incomes, and the amount of *pinhão* (in kg) collected on each property. Second, we used the *Sistema IBGE de Recuperação Automática* (SIDRA) (https://sidra.ibge.gov.br/pesquisa/pevs/tabelas) a public and open-access database from the Brazilian Institute of Geography and Statistics (Instituto Brasileiro de Geografia e Estatística), to collect several economic indicators and their historical series. We collected two *pinhão* historical series from 2010 to 2021 from Minas Gerais, Paraná, Santa Catarina, São Paulo, and Rio Grande do Sul states: (i) the amount of *pinhão* collected per year (tonnes) and (ii) the economic value of the *pinhão* annual trade (see https://sidra.ibge.gov.br/tabela/289).

2.4 Ethnoecological knowledge from an ecosystem services perspective

Ethnoecological information was also collected thanks to the semi-structured interviews. We collected information about the use, management, and knowledge of Brazilian Pine and its *pinhão* ethnovarieties. Leaning on smallholders' TEK, we collected evidence of the following: (i) ripening period, abundance, size, and color of *pinhão* ethnovarieties; (ii) the *pinhão* ethnovarieties known by each smallholder; (iii) the reproductive phenology and seed production of Brazilian Pine trees throughout the year; and (iv) the interviewees' perception about the potential impact of climate change on the Araucaria Forest, especially *A. angustifolia*. With this information, we created a framework to describe Brazilian Pine's ethnoecology: the ecosystem services provided by Brazilian Pine use and management, targeting four potential ecosystem services: provisioning, regulation, cultural, and support (following Bogoni et al. 2020a).

To generate the ecosystem services framework, defined by the Millennium Ecosystem Assessment (MEA) as the "benefits people obtain from ecosystems, promoting human well-being" (Millennium Ecosystem Assessment 2005), we created a binary matrix of *n*-smallholders by *m*-ecosystem services suggested. The total number of ecosystem services perceived by an interviewee from Brazilian Pine use and management was given by the sum of all ecosystem services perceived, following Machado et al. (2019). The ecosystem service categories (Bogoni et al. 2020a) and ecosystem services (Millennium Ecosystem Assessment 2005) that affect the well-being of people are the following: (i) provisioning (resource for human groups, such as food, wood, fiber, and water. Also, it includes phytodemographic dynamics that affect forest regeneration, such as seed predation and seed dispersal); (ii) regulation (climate regulation, disease control, insect pest control, natural disaster control); (iii) cultural (e.g., ethnocultural identity, ecotourism, aesthetics, education); and (iv) support (e.g., nutrient cycling, soil formation, primary production, oxygen). We cross-checked the interviewees' perceptions of ecosystem services with the literature to look for actual or possible ecosystem services provided by the Araucaria Forest system.

2.5 Quantifying the loss of ecosystem services of the Araucaria Forest system under climate change

To estimate potential losses of ecosystem services due to climate change throughout the Araucaria Forest system, we selected the latest peer-reviewed studies that show the impacts of future climate change on the Araucaria Forest (Table 1). We combined the studies' projections for 2050 and 2070 (Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020; Tagliari et al. 2021b) for the potential losses of climatically suitable areas ($\Delta Sloss$) for Brazilian Pine in the future under two climate change scenarios — Representative Concentration Pathways (RCP) 4.5 and 8.5 — to propose a baseline of "climate change impact." These four studies used both RCPs (4.5 and 8.5) because this has become common practice in species modelling approaches since they represent optimistic (RCP 4.5) and pessimistic (RCP 8.5) CO_2 emission scenarios (Riahi et al. 2011; Thomson et al. 2011). Thus, we

Table 1 References selected to estimate the potential threat of climate change to the Araucaria Forest system. We only selected peer-reviewed studies that calculated, under the species distribution modelling approach, the potential loss of climatically suitable areas for araucaria by 2050 and 2070 compared with current species potential occurrence. The Representative Concentration Pathways (RCPs) are CO_2 emission scenarios, where RCP 4.5 is an optimistic scenario that considers a mean increase of 1.4–1.8 °C by the late twenty-first century, whereas the RCP 8.5 is a realistic and pessimistic scenario where mean temperatures are expected to increase by 3.7 °C by the late twenty-first century (van Vuuren et al. 2011)

Reference		Loss of climatically suitable area in 2050 and 2070 compared to current Brazilian Pine distribution (%)		
Climate scenario	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Years	*2050*	*2050*	*2070*	*2070*
Wilson et al. (2019)	NA	NA	85.33	96.5
Castro et al. (2019)	NA	NA	27.7	60
Marchioro et al. (2020)	45	53	53	77
Tagliari et al. (2021b)	NA	NA	66.5	89
Projected loss (mean)	–		58.13%	80.62%
Projected average loss	49%		69.37%	

summed all projections (two for 2050 and eight for 2070) of area loss and divided them by the total amount of projections (*n*-projections) to get a value that represents the potential area loss of the Araucaria Forest system due to climate change (see Eq. 1). We defined the average loss of climatically suitable areas to evaluate how climate change could reduce the Araucaria Forest's suitable habitat in the future.

$$\sum RCP\,4.5\Delta S\,loss + \sum RCP\,8.5\Delta S\,loss \Big/ _{nprojections} \quad (1)$$

To quantify how climate change predictions could affect the ecosystem services provided within the Araucaria Forest, we analyzed adjacency matrices (Boccaletti et al. 2006). These matrices show the interaction networks between interviewees' ethnoecological knowledge and ecosystem services. According to the ensemble of model predictions of future suitable habitat change (Eq. 1) in the Araucaria Forest, we projected the *gain* or *loss* of ecosystem services within the studied area.

For each network (i.e., original and under climate changes scenarios), we obtained the following: (1) interviewed degree (Id), (2) ecosystem services degree (ESd), (3) connectance (C), (4) nestedness (N), and (5) modularity (M). The average degree (i.e., $\overline{\mathrm{X}}$Id and $\overline{\mathrm{X}}$ESd) describes the average number of interactions per interviewee and the putative ecosystem services in the network (Boccaletti et al. 2006). Connectance (C) represents the proportion of interactions (i.e., interviewed opinion vs. ES) observed in relation to the total possible interactions (Boccaletti et al. 2006). Modularity (M) quantifies the tendency of the nodes (interviewed–ESs) to form groups of vertices more connected to each other than to the other components of the network (Boccaletti et al. 2006). Nestedness (N) indicates a hierarchical pattern of interviewed-ES interactions, in which the less connected interviewed-ES interactions form a subset of the most connected interactions, representing a structural fitting (Almeida-Neto et al. 2008). We compared the metrics between the original adjacency matrix and climate change regimes, where any numerical change of the metrics suggests a loss of robustness or stability of the network of services provided by the Araucaria Forest system.

We assumed that the reduction of habitat suitability of Brazilian Pine is directly linked to the loss of ecosystem services provision because of the following: (i) its ecological keystone aspect in the ecosystem (Bogoni et al. 2020a); (ii) the already reduced natural remnants of the Araucaria Forest (Ribeiro et al. 2009; Rezende et al. 2018); (iii) *pinhão* gathering and araucaria productivity is linked to favorable climatic conditions, such as relatively cooler and moist conditions, and climate change will both warm and reduce rainfall patterns in the region, creating few hotspots for Brazilian Pine in the future — and these projected suitable areas have already been deforested (Wilson et al. 2019); and (iv) with projected reduction of *pinhão* productivity, it is expected that several gatherers and smallholders will shift their extractivism options and, consequently, the ethnoecological knowledge and management of this iconic tree species is indeed in the brink of disruption in the future.

3 Results

3.1 The potential loss of suitable habitat for the Araucaria Forest due to climate change

The four peer-reviewed studies showing the impacts of the potential habitat loss of Araucaria Forest due to climate change led to the conclusion that by 2070, climate change will shrink the Araucaria Forest system area by up to 69%. The RCP 8.5, which leans towards the most pessimistic climate previsions, predicts a loss of suitable area of up to 80%, while the RCP 4.5 — an optimistic climate projection — predicts a potential loss of suitable area of up to 58% compared to the original Araucaria Forest extent (Table 1). For 2050, the reduction of climatic suitable areas of the Araucaria Forest is expected to reduce 49%. Furthermore, no more than 10% of the projected distribution of the Araucaria Forest (i.e., currently or in the future) will be encompassed by existing protected areas according to these studies, which only considered Brazilian fully protected and sustainable use protected areas (*Proteção Integral* and *Áreas de Uso Sustentável*, respectively). These climatically suitable areas might also be encompassed by private protected areas, such as legal reserves and permanent preservation areas (*Reserva Legal* and *Área de Preservação Permanente*), as well as by Indigenous Territories. Finally, it is expected that the remaining forest will be restricted to more elevated areas.

3.2 Traditional ecological knowledge about pinhão and climate change

We identified 23 different *pinhão* ethnovarieties' descriptions based on 320 citations from all participants throughout southern and southeastern Brazil. These *pinhão* varieties were described by local smallholders, who are *pinhão* extractors, based on *pinhão* ripening periods by female Brazilian Pines. A cluster dendrogram was performed to assemble these different characteristics mentioned by local smallholders, such as color, shape, ripening period, size, and taste. The dendrogram indicated that seven *pinhão ethnovarieties* represent the clusters generated by these 320 citations: (i) "*Macaco*," (ii) "*25 de Março*," (iii) "*São José*," (iv) "*Cajuvá*," (v) "*Comum*," (vi) "*Do Cedo*," and (vii) "*Do Tarde*" (Fig. S1). The most cited *pinhão* ethnovarieties were the following: (i) "*Macaco*" ($N=81$ citations), (ii) "*Cajuvá*" ($N=80$ citations), (iii) "*Comum*" ($N=48$ citations), (iv) "*Do Cedo*" ($N=31$ citations), and (v) "*25 de Março*" ($N=16$ citations). Participants cited, on average, three ethnovarieties (52.5%) and another 25% described four ethnovarieties. The main ethnovarieties described by the participants were said to develop at different times of the year, suggesting *pinhão* production throughout the year, with the majority from March to December (Fig. 2). The ethnovarieties "*Do Cedo*" and "*Cajuvá*" were classified as the most abundant, which confirms that *pinhão* peak production occurs from March to July. "*Macaco*" is the rarest ethnovariety according to 67% of interviewees ($N=65$). We also recorded some new *pinhão* ethnovarieties in the study area. Usually, the "*Cajuvá*," "*Macaco*," "*Do Cedo*," and "*Do Tarde*" ethnovarieties are commonly described in the states of Paraná, Santa Catarina, and Rio Grande do Sul. However, in the municipality of Cunha (Mantiqueira Hills region at São Paulo state), the most frequently cited ethnovarieties were "*Caiano*" and "*Roxo*."

Interviewees were also asked to describe how they perceive the effects of climate change in the Araucaria Forest. Only eight interviewees did not answer this question, while 92% ($N=89$) believe that climate change will somehow impact the ecosystem. Increasing temperatures, milder winters, and less frost were the main aspects described by 74% ($N=66$) of the interviewees as the consequences of climate change. Climate unpredictability, such as anomalous or unstable winter and summer seasons, was also described as one of the main changes perceived throughout the landscape (46% or $N=41$). We also asked whether the Brazilian Pine tree would be affected by climate change. Among the 89 interviewees, 36 (40%) did not indicate that it will be affected by climate change, while for those who suggested climate change would influence araucaria species (53 interviewees),

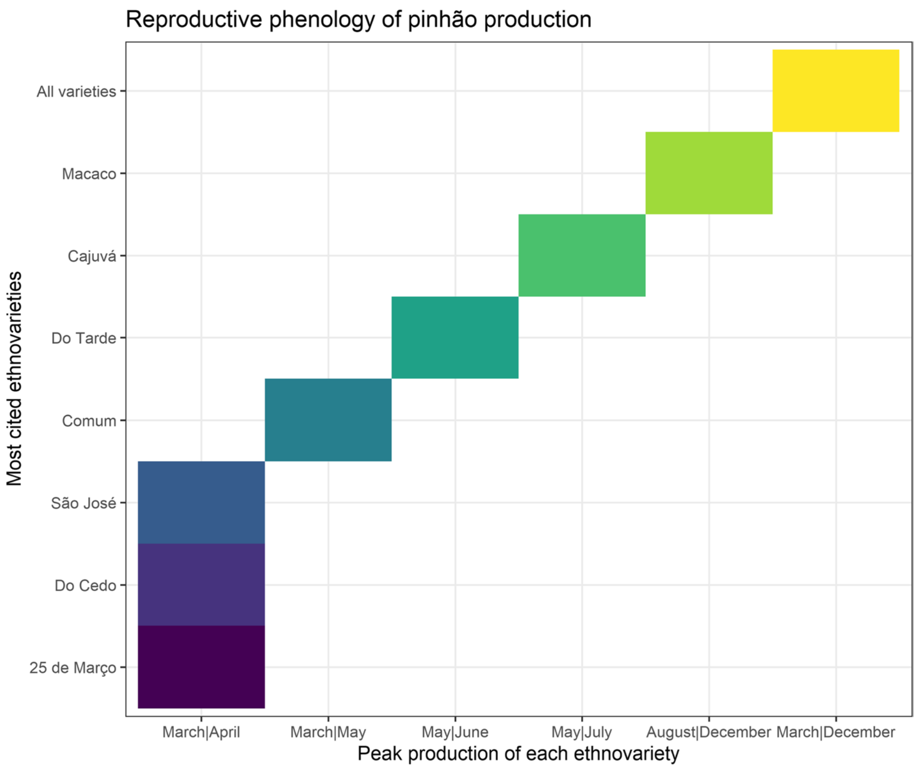

Fig. 2 The reproductive phenology of the main *pinhão* ethnovarieties during the year. The peak production of the first ethnovarieties is in March and April (*"25 de Março*," "*Do Cedo*," "*São José*"). For the two most cited ethnovarieties — "*Cajuvá*" and "*Macaco*" — peak production is from May to July and from August to December, respectively. *Pinhão* production for all varieties (yellow square) occurs from March to December

50% ($N=27$) believe the species will move to colder areas and 36% ($N=19$) stated the species will move to higher elevations (see Fig. 3 for a complete description about the perception of smallholders and *pinhão* extractors).

3.3 Socioeconomic benefits of *pinhão* extractivism

Pinhão extractivism and trade have been an alternative economic resource for smallholder families for at least 3.5 generations, and 65% of the 97 interviewees declared that *pinhão* trade contributes R $1000 to R $2500 to their monthly income; this was 1 to 2.3 times the Brazilian minimum wage in 2018, or US $253.8 to US $633.9 in 2019 (i.e., US $1 = R $3.94), according to the World Bank Indicator (https://data.worldbank.org/indicator/PA.NUS.FCRF?locations=BR). For 30% of the interviewees, the *pinhão* trade is their main annual income source. Typical crops, such as *yerba-mate*, tobacco, corn, and beans, are alternative income resources. *Pinhão* extraction is mainly done by men (95%, $N=92$). Women usually contribute by gathering *pinhão* beneath Brazilian Pine trees. Family groups might collect up to 10,000 kg of *pinhão* per year (11.5% or 11 people). Another 50% ($N=46$) commonly collects from 1000 to 10,000 kg per year. The economic value of the *pinhão* trade increased from 2010 to 2021 (Table 2). Brazilian southern states, Paraná,

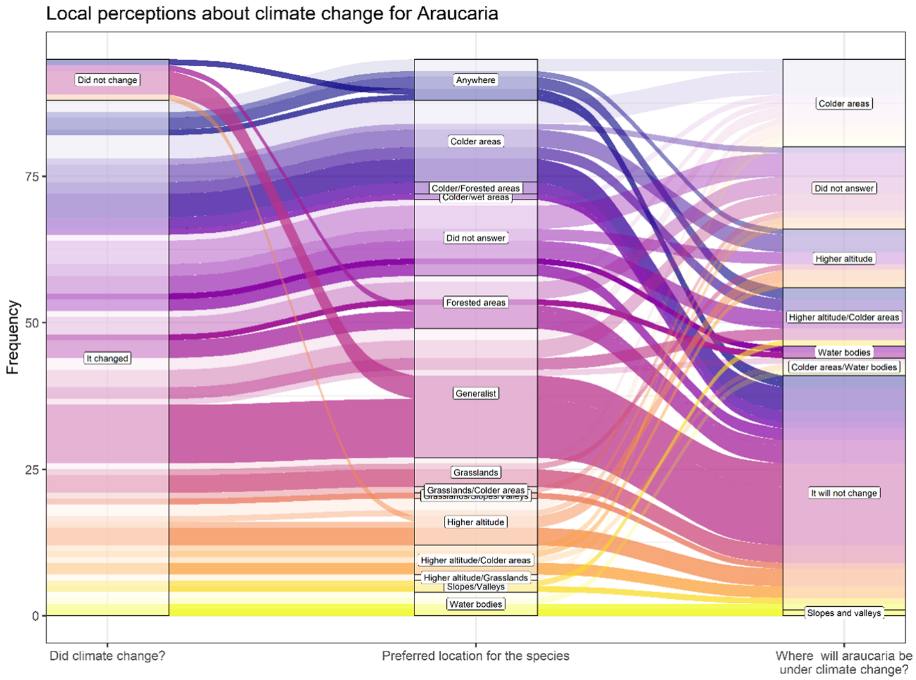

Fig. 3 The perceptions of TEK holders about the effect of climate change on araucaria and how this emblematic tree might respond to this disturbance. Different colors were used to facilitate comprehension from the reader

Santa Catarina, and Rio Grande do Sul, extract together, on average, 2,500,000 kg of *pinhão* per year. This amount represents approximately US $1,655,000, per year in Southern Brazil (Table 3). In southeastern Brazil, the states of São Paulo and Minas Gerais also benefit from the *pinhão* trade. Minas Gerais has been increasing *pinhão* extractivism, collecting 1,357,000 kg per year, totaling US $855,983.77 per year (Table 3), on average. For São Paulo State, both the amount collected and the monetary value of *pinhão* have

Table 2 The amount of *pinhão* harvested per year (kg * 1000) in the Brazilian states registered at CEASAS (perishable wholesale centers) between 2010 and 2021

Pinhão harvest between 2010 and 2021 (kg × 10³)												
Brazilian States	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Minas Gerais	276	164	87	323	1162	1213	1090	1288	1535	2139	3546	3464
São Paulo	355	6	6	6	6	6	6	6	6	5	5	5
Paraná	2536	4581	5932	3924	3582	3220	3183	3596	3373	3290	3671	4018
Santa Catarina	1799	2476	2790	3213	3147	3192	2663	3456	3621	3120	2537	3916
Rio Grande do Sul	749	806	823	828	881	762	805	947	1025	819	843	1081

Source: IBGE—Produção da Extração Vegetal e da Silvicultura. Available at: https://sidra.ibge.gov.br/pesquisa/pevs/tabelas

Table 3 The economic value of *pinhão* harvested per year (US$ * 1000) in the Brazilian states registered at CEASAS (perishable wholesale centers) between 2010 and 2021

Pinhão harvest between 2010–2021 (US$×10³)

Brazilian States	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Minas Gerais	137	73	20	65	471	517	457	505	622	955	2971	2767
São Paulo	297	2	4	4	4	4	5	5	6	6	9	13
Paraná	831	1666	2259	1790	1881	2034	2097	2524	2505	2598	3460	4340
Santa Catarina	771	707	983	1449	1943	2216	2335	1870	2231	2729	2811	2670
Rio Grande do Sul	278	333	393	482	606	606	793	922	957	897	1151	1392

Source: IBGE—Produção da Extração Vegetal e da Silvicultura. Available at: https://sidra.ibge.gov.br/pesquisa/pevs/tabelas

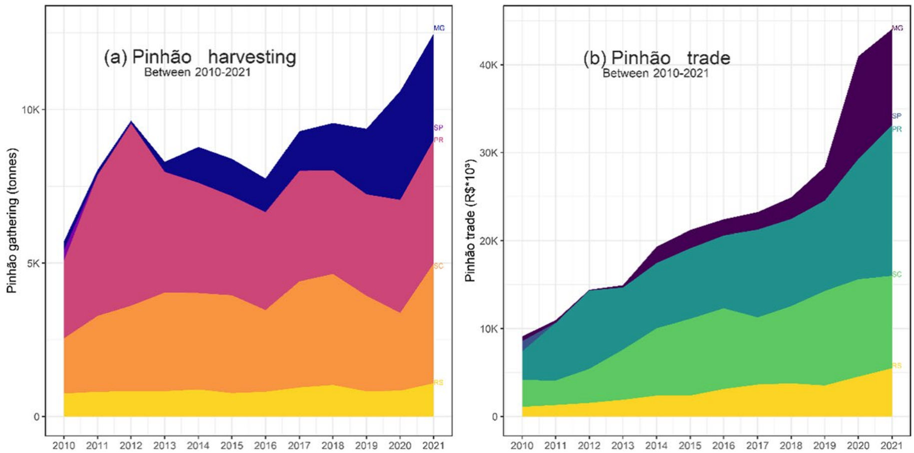

Fig. 4 **a** *Pinhão* harvesting (tonnes) and *pinhão* trade (in Brazilian R$) according to the 2010–2021 time series. Different colors represent each Brazilian State (i.e., Paraná (PR); Santa Catarina (SC); Rio Grande do Sul (RS); São Paulo (SP); Minas Gerais (MG) with available data at SIDRA webpage (https://sidra.ibge.gov.br/tabela/289). *Pinhão* harvesting indicates that all states collecting *pinhão* have gathered almost 15,000 tonnes in 2021. **b** The economic value indicates an increase of pinhão trade value since 2010 and a growing tendency in the future

not significantly changed, possibly because of the informal market of *pinhão* prior to the arrival at São Paulo CEASA (Fig. 4).

3.4 Perceptions of ecosystem services by TEK holders

The TEK holders' perceptions were grouped into 19 ecosystem services assigned to the following: (i) provision (resource for human groups, seed predation and dispersal, genetic resource, phytodemographic/forest dynamics); (ii) regulation (climate regulation, disease control, insect control, biological control, natural disaster control, pollination); (iii) cultural (ecotourism, ethnocultural identity, aesthetic, education); and (iv) support (soil formation, oxygen and nutrient cycling, primary production). TEK holders identified one to 14 ecosystem services (mean 3.94) among the four assigned services. The assigned ecosystem services (i.e., provision, regulation, cultural, and support) were described almost three times (mean 2.84) per TEK holder. The most frequently perceived ecosystem services were the following: (i) resource for human groups, due to *pinhão* use and trade ($N=96$); (ii) ethnocultural identity, because of the knowledge and description of ethnovarieties ($N=76$); (iii) climate regulation, due to their perception of Brazilian Pine phenology and potential climate change impacts on the ecosystem ($N=75$); (iv) phytodemographic dynamics, due to locals knowledge of species' ecological characteristics, such as seed dispersal, interspecific interactions, and its climatic niche ($N=40$); and (v) aesthetic, given the interaction of people with the environment based on human perceptions and judgments ($N=24$).

It is expected a potential loss of ecosystem services under climate scenarios because of the projected reduction of habitat suitability of *Araucaria angustifolia* (Fig. 5). The average ecosystem services degree according to our 97 interviews originally was $\overline{X}ESd_{Original}=22.95$. Assuming habitat suitability loss of 50% due to climate change in 2050, the potential ecosystem services might be reduced to $\overline{X}ESd_{2050}=11.84$. Under a potential loss of 70% of habitat suitability for the ecosystem predicted under future climate change scenarios, ecosystem services might be $\overline{X}ESd_{2070}=6.95$. The other network metrics (i.e., connectance, modularity, and nestedness) also reflect these projected losses. Connectance was

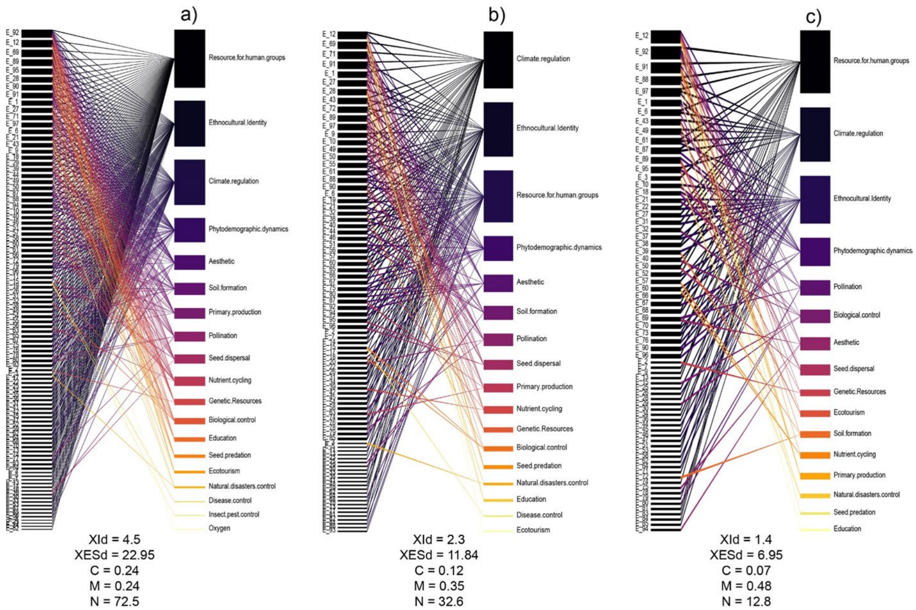

Fig. 5 **a** The perceptions of TEK holders (left column) about the ecosystem services (right column) provided by the Araucaria Forest. We represented all answers among the four main ecosystem services that affect the well-being of people: (i) provision (resource for human groups, seed predation, seed dispersal, phytodemographic dynamics); (ii) regulation (climate regulation, disease control, insect pest control, natural disaster control), (iii) cultural (e.g., ethnocultural identity, ecotourism, aesthetics, education), and (iv) support (e.g., nutrient cycling, soil formation, primary production, oxygen) following Bogoni et al. (2020a) to select the specific categories for each ecosystem service. To model the potential loss of the perception of ecosystem services due to climate change, we combined the outputs of the most recent peer-reviewed studies that estimated the potential area loss for araucaria by **b** 2050 (i.e., 50% loss of perceived ecosystem services) and **c** 2070 (i.e., 70% loss of perceived ecosystem services). Values are represented by interviewed degree (Id), ecosystem services degree (ESd), connectance (C), modularity (M), and nestedness (N)

originally $C_{Original}=0.24$ and decreased to $C_{2050}=0.12$ (50.0% reduction) and $C_{2070}=0.07$ (70.8% reduction). Modularity increased towards the future: $M_{Original}=0.24$; $M_{2050}=0.35$; and $M_{2070}=0.48$. The increase is caused by the formation of vertices more connected to each other rather to other components of the network. Finally, nestedness of our ecosystem services network might decrease as well: $N_{Original}=72.5$ in the present; $N_{2050}=32.6$ in 2050 (55% reduction); and $N_{2070}=12.8$ in 2070 (82.5% reduction; Fig. 5).

4 Discussion

4.1 The potential loss of Araucaria Forest due to climate change and its impacts from a holistic perspective

Using the most recent studies about the effects of climate change on *A. angustifolia* and, consequently, to the entire SES of the Araucaria Forest in Brazil, we showed the main socioeconomic, ethnoecological, and ecological aspects that might be at risk under both medium- (2050) and long-term (2070) climate change scenarios. We found evidence using an ethnoecological approach that smallholders and *pinhão* extractors, who use, manage, differentiate *pinhão* ethnovarieties, and/or sell *pinhão*, provide several ecosystem services, from provisioning services, given the preservation of the Araucaria Forest ecosystem, to cultural aspects, thanks to the ethnocultural identity of local peoples. If this vulnerable group is undermined by the effects of global change, due to the reduction of suitable habitat for the Brazilian Pine, the entire SES might be doomed. Smallholders and *pinhão* extractors fall within the definition of family farming: where the property management is shared by family members and the pre-defined agricultural crop is the main source of income (Brasil 2017). According to *Censo Agro 2017* from IBGE (available at: https://censoagro2017.ibge.gov.br/resultados-censo-agro-2017.html), almost 25% of all Brazilian agricultural establishments are family farming. Almost 40% of southern states (RS, SC, PR) agricultural production value comes from family farming. There is a strong link, consequently, between Araucaria Forest conservation and local human groups. By understanding the effects of biodiversity loss on human well-being as quantified in the framework of ecosystem services perspective, we presented a valuable contribution using an ecological (Bogoni et al. 2020a) and "cultural keystone" (sensu Garibaldi and Turner 2004) species as the main proxy in the Araucaria Forest SES.

4.2 Brazilian Pine ethnovarieties as an ecological keystone resource

Besides its umbrella and nurse effects, which structure the overstory ecosystem, increase sapling richness, and promote plant species diversity, regeneration, and development under its canopy (Reis et al. 2018; Sühs et al. 2018), *A. angustifolia* is also of pivotal importance in maintaining the faunal community and its diversity. Its available resource (*pinhão*) provides the following to local fauna: (i) low temporal redundancy (i.e., few other plant resources are available when *pinhão* is available); (ii) low consumer specificity (i.e., *pinhão* is usually consumed by different species); (iii) high resource reliability (i.e., the staggered availability of *pinhão* throughout the year); and (iv) resource abundance (i.e., high production of *pinhão*). Consequently, the Brazilian Pine structures the associated consumers spatiotemporally (Bogoni et al. 2020a), such as mammals (*Dasyprocta azarae*, *Delomys dorsalis*, *Oligoryzomys nigripes*, *Procyon cancrivorus*, *Tayassu pecari*) and birds, for example, *Amazona vinacea*, *A. pretrei*, *Cyanocorax caeruleus*, and *C. chrysops* (Iob and Vieira 2008; Montagna et al. 2019).

By identifying the *pinhão* ethnovarieties and their peak production periods during the year, which is mainly between March and December, we also suggest that both aspects of keystone plant resources, (i) high resource reliability and (ii) resource abundance production, might be a consequence of the historical domestication process of this species by human groups. "*Macaco*," on one hand, is usually described as the "rarest" and "smallest" *pinhão* ethnovariety, but it produces *pinhão* throughout the whole year (Adan et al. 2016; Tagliari and Peroni 2018). The most abundant variety ("*Cajuvá*"), on the other hand, is commonly described as the "*biggest*" or "*tastiest*" *pinhão* variety (Adan et al. 2016; Tagliari and Peroni 2018). We believe that both the reproductive phenology and ethnovariety characteristics of Brazilian Pine are consequences of the domestication process and the use of Brazilian Pine resources since the time of pre-colonial Amerindians (Cruz et al. 2020) benefits and structures both the fauna and flora in the Araucaria Forest system.

Forest management in the Araucaria Forest system region for the past 1400 years expanded this forest beyond its natural extent resulting in areas with an elevated demography (Robinson et al. 2018). We argue that the current use and knowledge of Brazilian Pine ethnovarieties still shape and maintain the productivity and conservation of this ecosystem from a landscape domestication perspective (Reis et al. 2018), where management practices, the species demographic structure, and its genetic diversity reinforce this concept (Reis et al. 2018). These forest management practices occur mainly at smallholders' Legal Reserves, where more than 30% or Araucaria Forest remnants are expected to be located (Metzger et al. 2019). Consequently, smallholders managing *pinhão* ethnovarieties bridge ecological interactions with protected areas, such as reducing the impacts of forest fragmentation (Ribeiro et al. 2009), as well as spatial and temporal patterns of forest stands, where managed remnants might be human modified thanks to female Brazilian Pine selection for ethnovarieties production, whereas protected areas maintain biodiversity and potentially increases genetic flow between managed and non-managed patches. Assuming, thus, that climate change might drastically reduce the habitat suitability of Brazilian Pine by 2070 (Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020; Tagliari et al. 2021b), this effect might ruin critical ecological interactions, as well as collapse the current human-plant interactions.

4.3 Socioeconomic impact and declines in ecosystem services

The current human-plant interactions result in economic profits not only to local smallholders and *pinhão* extractors but to an entire network extending to the final consumers (Vieira-da-Silva and Miguel 2017). The SIDRA historical series of *pinhão* trade and consumption (see Tables 1 and 2) only accounts for the *pinhão* traded at Brazilian CEASAS (*perishable wholesale centers*). However, there is an "informal" market for *pinhão* that does not involve CEASAS and is not accounted for in the historical series. This informal market is mostly linked to local landowners and people who sell *pinhão* along Brazilian state highways, supplying markets in smaller cities, mainly in the highlands of southern Brazil and specific regions in the Mantiqueira hills in the southeastern portion of the country (Adan et al. 2016; Tagliari and Peroni 2018; Quinteiro et al. 2019). The vertiginous increase in the value of *pinhão* per year in Brazil (Fig. 4b) and the amount collected per year (Fig. 4a) reveal that *pinhão* harvesting has not reach its limit, especially in the last 2 years (2020 and 2021). Uncontrolled *pinhão* harvesting done by smallholders and *pinhão* extractors is exclusively via extractivism, which might be dangerous once there is a critical intensity threshold of nut harvesting between 60 and 85% (Fichino et al. 2017). By exceeding this threshold, uncontrolled *pinhão* harvesting might prevent, in both short and long term, Brazilian Pine regeneration, as well as limit and reduce ecosystem services, such as provision (*pinhão* provisioning), support (primary production), and regulation (carbon sequestration) (Fichino et al. 2017). On one hand, according to Fichino et al. (2017), the harvesting threshold below 60% indicates no financial compensation for *pinhão* harvesters, and on the other hand, when harvesting pressure threshold is higher than 85%, there is a negative correlation with the number of seedlings, germinated *pinhão*, and local fauna interaction, indicating that harvesting activity might be jeopardized.

The very few regulations for *pinhão* harvesting are limited to when the extraction season begins. This is usually on 1 April in the states of Paraná and Santa Catarina or 15 April in the state of Rio Grande do Sul; we found no information for the states of São Paulo and Minas Gerais. However, the majority of extractors usually gather and trade *pinhão* for financial subsistence and food security, and not to guarantee the conservation of the species, ecosystem maintenance, or sustainable harvesting (Adan et al. 2016; Tagliari and Peroni 2018; Quinteiro et al. 2019; Tagliari et al. 2021a). The lack of environmental incentives, especially via payment for ecosystem services (Tagliari et al. 2019), leads, especially for landowners, to antagonistic conservation practices, such as Brazilian Pine seedling suppression (Tagliari and Peroni 2018; Schneider et al. 2018; Quinteiro et al. 2019). It is widely documented that TEK holders claim public incentives that values their management practices within the Araucaria Forest (Adan et al. 2016; Tagliari and Peroni 2018; Quinteiro et al. 2019) since these socioeconomic and ecological interactions promote gene flow (Zechini et al. 2018), genetic diversity (Montagna et al. 2019) and intraspecific diversity for Brazilian Pine populations (Mello and Peroni 2015; Adan et al. 2016; Reis et al. 2018; Quinteiro et al. 2019), perpetuation of productive forest remnants via “conservation-by-use” (Reis et al. 2018), and the maintenance or even the expansion of the entire socio-ecological system via positive feedbacks (Tagliari et al. 2021a).

Due to climate change, however, TEK holders might be even more vulnerable because of their dependence on climatic conditions (Holland et al. 2017). In the Araucaria Forest system, TEK holders usually live with food insecurity and precarious conditions, exacerbating their socioeconomic vulnerability. The imminent impacts of climate change both in the short and long term within the Araucaria Forest, especially on *A. angustifolia* habitat suitability (Castro et al. 2019; Wilson et al. 2019; Marchioro et al. 2020), might trigger potential cascading effects to the entire socio-ecological system, affecting one of the major contributors to the balance of this SES.

Given that ecological network is a tool to understand, depict, and predict ecosystem functioning, species interactions, and ecological functions (Boccaletti et al. 2006), the ecosystem services provided by the Araucaria Forest might be undermined, thus compromising human well-being. For instance, the presumed ecosystem services degree could decline by 70% by 2070. The ecological network of ecosystem services perceived by smallholders based on their TEK could also be threatened because climate change decreases all the metrics, such as connectance and nestedness (65% loss on average). The increase in modularity can indicate dense connections within the nodes in every cluster in 2070 but with a sparse connection between different nodes (i.e., the perception of ES could be shared by subgroups of people, but not shared by the group as a whole). Empirical evidence indicates a similar pattern in decline of ecosystem services and network rearrangements due to mammal defaunation scenarios (Bogoni et al. 2020b).

4.4 Food security and sociocultural interconnections with the Araucaria Forest system

Climate change projections and the potential reduction of the distribution of Brazilian Pine are major concerns for local communities and their food security. The *pinhão* from Brazilian Pine is a nutrient-rich food resource that contains several minerals (e.g., potassium, phosphorus, and manganese; Barbosa et al. 2019). Since it is a typical regional resource, which guarantees both economic and dietary security to local human groups, strengthening the traditional use and management of local food resources might also preserve local keystone species (Tagliari et al. 2021b). Also, this would support the maintenance and aesthetic connections of the cultures of peoples, and how human groups perceive and incorporate a sense of belonging with the surrounding environment.

5 Conclusion

5.1 Araucaria Forest contributions to people and the contribution of people to the Araucaria Forest: the pathway to promote resilience to climate change

Several aspects must be considered to promote resilience within the Araucaria Forest system. The first is the cornerstone of conservation: protected areas (Rodrigues and Cazalis 2020). The Araucaria Forest originally covered more than 1,118,000 km^2. Optimistic projections indicated that only 10 to 24% of this ecosystem still stands (Ribeiro et al. 2009; Rezende et al. 2018) and barely 10.3% of these remnant areas are protected (Indigenous Territories cover only 0.72% or 8,050 km^2). These protected areas are 25% classified as strictly protected areas and 75% as sustainable use areas (Pacheco et al. 2018). Within the sustainable use areas, two categories could potentially benefit TEK holders within the Araucaria Forest: sustainable development reserves (RDS) and extractive reserves (RESEX). However, of the 75% classified as sustainable use areas, just 1.07% is classified as RDS or RESEX, while 72% is classified as environmental protection areas (Pacheco et al. 2018), which do not benefit local peoples. Concerning *A. angustifolia*, no more than 5 to 10% of its predicted suitable areas in the future (i.e., which are expected to decrease by ≦70% by 2070) will be encompassed by the existing protected area network (Castro et al. 2019; Marchioro et al. 2020; Tagliari et al. 2021b). These suitable habitat areas non-protected in the future will be at more elevated, moister, and colder areas (Castro et al. 2019; Wilson et al. 2019; Bergamin et al. 2019; Marchioro et al. 2020), as TEK holders also described in this study (Fig. 3). Consequently, the first conservation priority as a response to climate change is to identify these potential areas and create new protected areas, as well as creating RESEX and RDS sustainable use areas where large TEK holder groups coexist.

The second major aspect is targeting the main actors in this socio-ecological system: TEK holders. Different potential strategies must be implemented to reinforce and maintain this human-plant interaction under the payment for ecosystem services framework: (i) conservation of forest stands beyond the legally required minimum area; (ii) valuation of the *pinhão* supply chain; (iii) maintenance of *pinhão* ethnovarieties; (iv) mensuration of the ecosystem services provided by remnant areas; (v) restoration of degraded areas; and (vi) food security for vulnerable social groups (see Tagliari et al. 2019 for an evaluation of different payment for ecosystem services programs in southern Brazil). Also, recent studies shed light on the possibility of sustainable timber exploitation as a strategy to engage local people (Orellana and Vanclay 2018; Montagna et al. 2019). Hence, by valuing these actors, Brazilian Pine intraspecific and functional diversity are boosted and, consequently, promote resilience and adaptive capacity to climate change, besides creating positive feedback between TEK holders and the entire socio-ecological system (Elmqvist et al. 2003; Holland et al. 2017; Tagliari et al. 2021a). Furthermore, by preserving Brazilian Pine remnants via TEK holders, we find a win–win strategy because there is the possibility of engaging more local groups in environmental governance and reducing actions that degrade the surrounding environment thanks to restrictive measures that usually exclude local groups (Tam and Chan 2017; Orellana and Vanclay 2018; Zechini et al. 2018; Tagliari et al. 2021a).

We do not expect, however, to treat TEK holders as a new panacea to fight against climate change. But, especially for socio-ecological systems worldwide, there is a necessity to implement holistic, integrative, and non-mutually exclusive conservation measures using top-down (such as restrictive legislation or strict use protected areas) to bottom-up (such as collaborative management initiatives with traditional human groups, payment for ecosystem services projects, or sustainable use protected areas) strategies. By using these integrative approaches, we might reinforce resilience and adaptive capacity to anthropic disturbances in the Araucaria Forest. Otherwise, if we do not seek an integrative response, this valuable socio-ecological system might be disrupted by climate change.

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Author contribution MMT conceived the study. MMT and JAB wrote the original draft of the manuscript and conceived the main statistical analysis. MMT, JAB, GDB, APC, and NP contributed equally to the main aspects of the research: literature review, statistical analysis, and manuscript revisions. All authors edited and approved the manuscript.

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Data availability The R code to entirely reproduce the output of this study is available on GitHub: https://github.com/masemuta/disruption_af. Table data are freely available on the SIDRA – IBGE website. Due to ethical aspects, we will provide the ethnoecological data under reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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