Chapter 9

Tetrapod Diversity in the Atlantic Forest: Maps and Gaps

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Abstract The Atlantic Forest is a heterogeneous and complex vegetation mosaic caused by variety of climatic, geomorphological, and edaphic conditions. It has long been known that the Atlantic Forest has one of the most diversified biotas on the planet, presenting high levels of endemism. Here, we update the knowledge regarding terrestrial vertebrates occurring in the Atlantic Forest, focusing on endemic species and presenting its main spatial patterns of diversity. We also analyzed the main knowledge gaps associated with these species. We identified 2,645 species of Tetrapoda in the Atlantic Forest, being 719 species of amphibians, 517 species of reptiles, 1,025 species of birds, and 384 species of mammals. The uniqueness of its fauna is impressive even in a global scale, as 2.8% of the world's Tetrapoda species occurs only in the Atlantic Forest. For reptiles, this percentage is 1.3%, while for both birds and mammals, it hovers around 1.9%, but for amphibians, it reaches an impressive 6.6%. Spatially, most groups exhibit their highest species

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richness at the core of the Atlantic Forest, and this pattern becomes more evident when only endemic species are considered. Even with all its impressive diversity, 157 new Tetrapoda species were described in the Atlantic Forest in the last decade, mostly from poorly sampled regions or environments. An increase of sampling effort on these regions might increase the number of species on this biome, which already is one of the most diverse in the world.

Keywords Endemism · Linnean shortfall · Richness · Spatial patterns · Wallacean shortfall

9.1 Overview

The Atlantic Forest is among the largest blocks of tropical forests of the world and the second largest rainforest in South America (Sobral-Souza and Lima-Ribeiro 2017), once covering more than 1.3 million km^2 (Paglia and Pinto 2010). It stretches from northeastern Brazil to northern Argentina and eastern Paraguay, comprising a variety of climatic, geomorphological, and edaphic conditions that result from this wide latitudinal, longitudinal, and altitudinal range (Ribeiro et al. 2011). There is a longitudinal gradient strongly correlated with precipitation, running inland from the coast, that results in a gradient between evergreen and semideciduous forests. Simultaneously, there are latitudinal and altitudinal gradients associated with both temperature and rainfall, resulting in a variety of forest formations, such as the subtropical *Araucaria* moist forest, cloud forest, and montane forest (Oliveira-Filho and Fontes 2000; Eisenlohr and Oliveira-Filho 2015). The Atlantic Forest is a complex vegetation mosaic composed of many distinct phytophysiognomies. Although much of the Atlantic Forest was originally covered by forests, other types of vegetation are also found within the ecoregion, such as the *campos rupestres*, *campos de altitude*, mangroves, and sand coastal plains or *restingas* (Scarano 2002).

During its evolutionary history, the Atlantic Forest was repeatedly connected to the Amazon (Vivo and Carmignotto 2004; Sobral-Souza et al. 2015; Ledo and Colli 2017), with eventual dispersal and biotic interchange between these ecoregions (Costa 2003; Lynch Alfaro et al. 2012; Buckner et al. 2015). These connections were followed by periods of isolation with subsequent allopatric speciation (Silva et al. 2004). The Atlantic Forest also experienced other major geological events and environmental changes, such as the establishment of major river systems, the uplift of the Serra do Mar (Safford 1999), and sea level changes (Leite et al. 2016), which influenced biological diversification (Costa 2003; Pellegrino et al. 2005; Sobral-Souza and Lima-Ribeiro 2017; Figueiredo and Grelle 2018). Its complex evolutionary history, coupled with the high environmental heterogeneity, is the main factor associated with the high levels of diversity and endemism of the Atlantic Forest (Sobral-Souza and Lima-Ribeiro 2017).

The Atlantic Forest has one of the most diversified biotas on the planet, comprising 1–8% of the world's biodiversity (Silva and Casteleti 2003) and more than 5% of the world's vertebrates (Paglia and Pinto 2010). A previous assessment of the Tetrapoda diversity in the Atlantic Forest includes 990 species of birds, 370 amphibians, 295 mammals, and 200 reptiles, in a total of 1,855 species of terrestrial vertebrates (Paglia and Pinto 2010), while another assessment includes 861 species of birds, 625 amphibians, 321 mammals, and approximately 300 reptiles, in an approximate total of 2,107 species of Tetrapoda (Monteiro-Filho and Conte 2017). Its biota is also very distinct, with endemism rates ranging from 25% in birds to 78% in amphibians (Monteiro-Filho and Conte 2017), and 2% of all vertebrates are endemic to the Atlantic Forest (Myers et al. 2000).

New information is now available to better describe Atlantic Forest vertebrate diversity, as new species were described and databases became available. Herein, we summarize and update the knowledge regarding terrestrial vertebrates occurring in the Atlantic Forest, focusing on endemic species and describing spatial patterns of diversity. We examine and discuss the main knowledge gaps associated with these species.

9.2 Endemism

To obtain a list of occurring and endemic species of terrestrial vertebrates, we used the integrative limit of the Atlantic Forest following Muylaert et al. (2018). This limit is comprehensive and inclusive, because it includes Atlantic Forest remnants occurring today in ecotone or enclave condition, as is the case of the *Brejos de Altitude* humid forest enclaves, in the Caatinga ecoregion. These remnants are important as a register of the diversity of plants and animals that once were part of the Atlantic Forest and are currently distributed in other biomes, serving as an evidence of some patterns of historical biogeography.

First, we performed a spatial overlay between the integrative limit and the specialist-drawn geographic distribution maps of reptiles (Meiri et al. 2017), birds (BirdLife International and NatureServe 2011), amphibians, and mammals (IUCN 2014), which were drawn by specialists and are available in digital format. All species whose distribution intersected with the limit of the Atlantic Forest were considered as occurring in this ecoregion. We gave preference to maps which represented the historical geographic distribution of the species. In addition to the digital maps, we also conducted a non-systematic search of the literature for newly described species. From those sources, we formed our list of species occurring in the ecoregion. To identify the endemic species, we followed a criteria applied by Vale et al. (2018) and defined as endemics those species that have at least 80% of their distribution within the limit of the Atlantic Forest.

We projected the digital distribution maps over an equal-area hexagonal grid (~500 km^2 cells) that encompassed the entire Atlantic Forest and obtained a list of all species present in each cell. Based on this list, we estimated total and endemic species richness for each cell of the hexagonal grid. We also estimated the restricted-range richness, which is richness estimative weighted by the range size of each species. It was defined as the sum of the inverse of the geographic range size of all endemic species present in a cell, as species with restricted geographic ranges contributed more to this index than those with large geographic ranges.

As species with distinct ecological requirements may respond to the environment in different ways, we chose to use a deconstructive approach of diversity (Marquet et al. 2004) to better represent the spatial patterns of diversity in the Atlantic Forest. That is, we first provide summaries for the major groups of terrestrial vertebrates (amphibians, reptiles, birds, mammals) and then proceed to progressively more restricted taxonomic subgroups (e.g., anurans, caecilians, turtles, lizards, snakes, amphisbaenids, crocodilians, nonpasserine birds, passerine birds, terrestrial mammals, and bats).

The subgroup anurans include all species of the order Anura, while the caecilians include all species of the order Gymnophiona. The subgroup turtles include all species of the order Testudines, while the crocodilians include all species of the order Crocodylia, and the amphisbaenids include all species of the family Amphisbaenidae. The subgroup lizards include all species of the families Dactyloidae, Diploglossidae, Gekkonidae, Gymnophthalmidae, Hoplocercidae, Iguanidae, Leiosauridae, Liolaemidae, Phyllodactylidae, Polychrotidae, Scincidae, Sphaerodactylidae, Teiidae, and Tropiduridae. The subgroup snakes include all species of the families Aniliidae, Anomalepididae, Boidae, Colubridae, Elapidae, Leptotyphlopidae, Tropidophiidae, Typhlopidae, and Viperidae. The subgroup passerine birds include all species of the order Passeriformes, while the subgroup nonpasserine birds include the species of all the other orders of the class Aves. The subgroup bats include all species of the order Chiroptera, while the subgroup terrestrial mammals include the species of all the other orders of the class Mammalia.

9.3 Tetrapod Diversity

We identified 2,645 species of Tetrapoda in the Atlantic Forest, comprising 719 species of amphibians, 517 reptiles, 1,025 birds, and 384 mammals. Thus, the Atlantic Forest comprises one of the most diverse ecoregions on the planet, with 9.5% of all amphibians, 5.1% of reptiles, 9.2% of birds, 6.7% of mammals, and 7.7% of all Tetrapoda species of the world (Table 9.1). With recent studies and our definition of Atlantic Forest residents, the number of species of birds increased somewhat, while the number of species of mammals, amphibians, and, especially, reptiles increased much more as compared to previous studies (Paglia and Pinto 2010).

The tetrapod fauna uniqueness in the Atlantic Forest justifies its designation as an important biodiversity hotspot (Myers et al. 2000). One in three species of Tetrapoda (36%) in the Atlantic Forest is endemic. Even so, endemism is uneven among taxonomic groups, reaching 70% for amphibians, while the other three groups range from 20% to 30% (Table 9.1). This uniqueness extends to the global

Table 9.1 Species diversity and endemism of the four major groups of tetrapods in the Atlantic Forest. The first three columns are total numbers of species. The next two columns are the proportions of the global total found in the Atlantic Forest. The final column is the percentage of Atlantic Forest species that are endemic. The sources used for the numbers of described species in the world are Jetz and Pyron (2018) for amphibians, Roll et al. (2017) for reptiles, BirdLife International (2018) for birds, and Faurby and Svenning (2015) for mammals

	Number of species			Relative number of species (percentage of total)		
	Atlantic Forest		World	World		Atlantic Forest Endemic
Taxonomic group	Total	Endemic		Total	Endemic	
Amphibian	719	504	≈7,600	9.5	6.6	70.1
Reptile	517	126	10,064	5.1	1.3	24.4
Bird	1,025	215	11,126	9.2	1.9	21.0
Mammal	384	109	5747	6.7	1.9	28.4
Tetrapoda	2,645	954	34,537	7.7	2.8	36.0

scale, because for every forty species of tetrapod in the world, one (2.7%) is found only in the Atlantic Forest, compared to 2% as estimated by Myers et al. (2000). Amphibians are very unique, with 6.6% of the global total of species being endemic to the Atlantic Forest. Endemic reptiles comprise 1.3%, while endemic birds and mammals are 1.9% of the global total of species (Table 9.1). A complete list of species which occur at the Atlantic Forest is available in the Supplementary Material.

As observed in these major groups, endemism is variable among subgroups. A high level of endemism is associated to some subgroups, where more than 70% of the species of caecilians and anurans (Amphibia) and half (50%) of the species of amphisbaenids are endemic to the Atlantic Forest. There are subgroups with moderate levels of endemism, where 38% of terrestrial mammals, 27% of passerine birds, and ~20% of snakes and lizards are endemic. The turtles, nonpasserine birds, and bats have fewer endemics (<15%), with no crocodilians being endemic (Table 9.2).

9.3.1 Spatial Patterns of Diversity

In describing distributions, we excluded caecilians and crocodilians because they are represented by too few species (ten, four, respectively) to provide meaningful maps. Because anurans comprise more than 98% of all amphibians, we simply joined all amphibians in one map. Spatial variation in species richness follows a well-known geographic pattern, with the greatest number of species at the center of the ecoregion: in the mountainous region of the Serra do Mar, decreasing toward the extremes (Fig. 9.1). This distribution pattern is clearly discernable in amphibians, birds, mammals, and most of their subgroups, including nonpasserines, passerines, and terrestrial mammals. Bats were the exception with a clear gradient of increasing species richness toward the equator. This pattern of increased species richness

Table 9.2 Diversity and endemism of the Atlantic Forest's species of Tetrapoda, presented by subgroups of species that share taxonomic affiliation and/or ecological function

	Number of species	Number of endemics	Percentage of endemics
Amphibia			
Caecilians	12	9	75.0
Anurans	707	495	70.0
Reptilia			
Snakes	278	64	23.0
Lizards	174	39	22.4
Turtles	21	3	14.3
Crocodilians	4	0	0.0
Amphisbaenids	40	20	50.0
Aves			
Nonpasserines	449	59	13.1
Passerines	576	156	27.1
Mammalia			
Terrestrial mammals	262	101	38.5
Bats	122	8	6.6

toward the core of the Atlantic Forest is well-known (Costa et al. 2000; Campos et al. 2017; Vale et al. 2018) and is usually associated with the topographic variability in the Serra do Mar. Due to this variable topographic relief, mountainous regions present strong environmental gradients and spatial heterogeneity over short geographic distances (Janzen 1967; Ruggiero and Hawkins 2008) that together favor greater speciation rates (Fine 2015) and species turnover, resulting in greater overall diversity (Melo et al. 2009).

Reptiles, in turn, have contrasting patterns, with greater species richness in the semideciduous forests of the states of São Paulo and Minas Gerais (Fig. 9.1), in a contact zone with the Cerrado ecoregion. Contrary of other Tetrapoda, reptile species richness was not congruent among subgroups. Species richness of lizards was greatest in the dry forests around the Caatinga, while amphisbaenid diversity was greatest in the westernmost portions of the Atlantic Forest, and turtles showed a pattern similar to that of all tetrapods.

When considered only endemic species, different distribution patterns by taxonomic group all disappeared. While the exact center of richness varied somewhat, most endemic groups were more species-rich in the core areas of the Atlantic Forest, in the Serra do Mar region (Fig. 9.2). Two subgroups diverged somewhat from this pattern, with amphisbaenids and bats (both of which with few endemics, 19 and 9, respectively) that had more than one peak of species richness (Fig. 9.2). Restricted-range species richness distributions tended to be similar to those of endemic species, with most groups being most diverse in the Serra do Mar region, with some notable exceptions in the northeast (Fig. 9.3).

Larger versions of the individual maps combined in Figs. 9.1, 9.2, 9.3 and 9.4 are available in the Supplementary Materials.

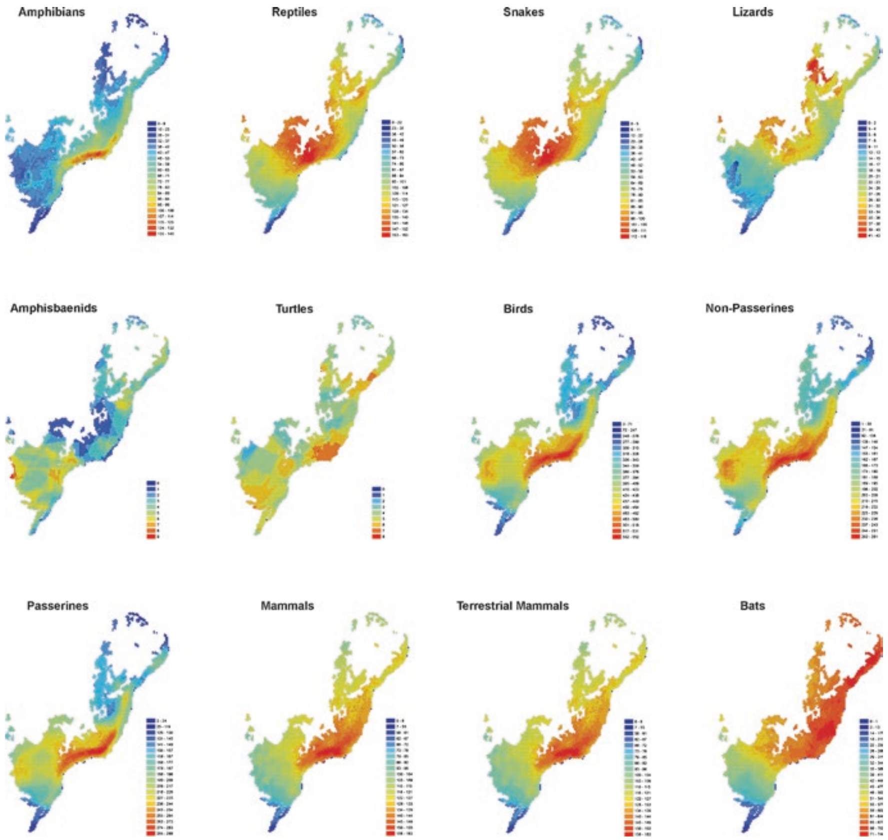

Fig. 9.1 Distribution of observed species richness for all the groups and subgroups of terrestrial vertebrates in the Atlantic Forest, mapped to a 500 km^2 resolution equal-area (Albers) projection grid. The gradient runs from dark red, which indicates the high-richness areas, to dark blue which indicates the low-richness areas

9.4 Knowledge Quality

Any analysis of large-scale patterns of diversity must consider the extent of our knowledge regarding biodiversity itself. The unevenness in sampling effort and the lack of adequate taxonomy result in high spatial variation in the quality and reliability of the data available. This compromises our ability to find and interpret biodiversity patterns, as we work with limited and often biased information (Riddle et al. 2011). These gaps in knowledge, also known as shortfalls, are related to limited information regarding species' taxonomy, ecology, evolution, and/or biogeography (Hortal et al. 2015). There are seven identified shortfalls, two of them have preponderant effects on large-scale patterns of diversity. We discuss these two shortfalls below.

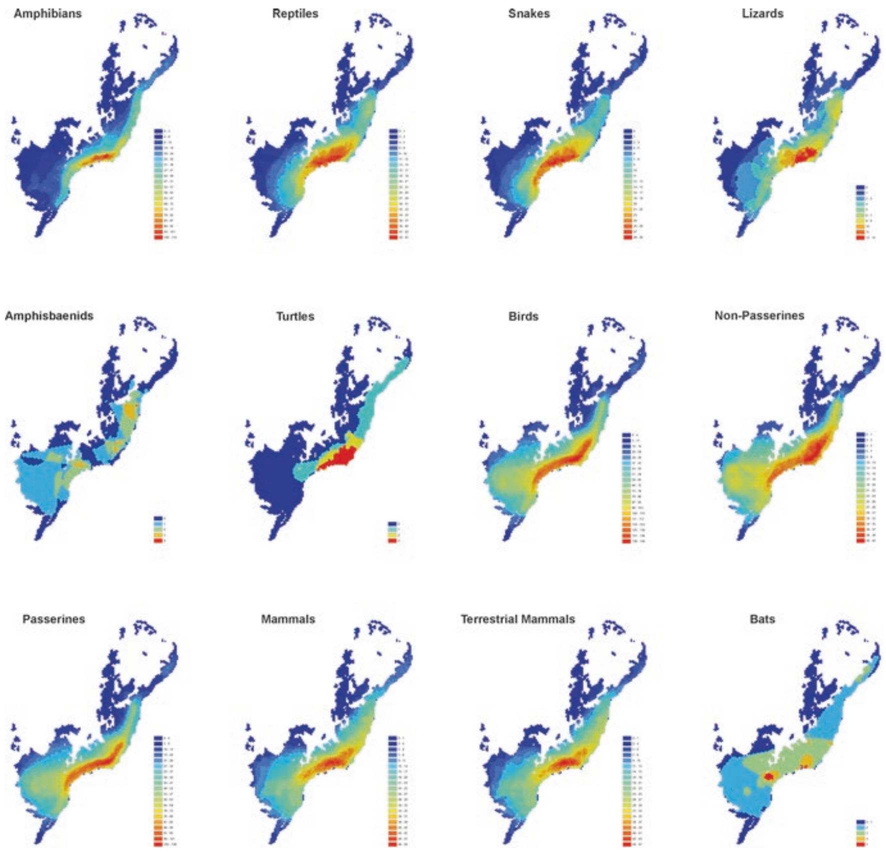

Fig. 9.2 Distribution of observed endemic species richness for all the groups and subgroups of terrestrial vertebrates in the Atlantic Forest, mapped to a 500 km^2 resolution equal-area (Albers) projection grid. The gradient runs from dark red, which indicates the high-richness areas, to dark blue which indicates the low-richness areas

9.4.1 Linnean Shortfall

This is the first shortfall and refers to the discrepancy between the number of described (and named) species and the estimated number of species that actually exist (Raven and Wilson 1992). The magnitude of the Linnean shortfall is unknown for many reasons, the main one of which is that we cannot rely on an accurate estimate of unknown species. In practice, the number of formally described species changes constantly as a result of new descriptions and taxonomic revisions. There are two categories of unknown species: those yet to be sampled and those sampled but yet to be described. Both categories influence our knowledge of the tetrapods of the Atlantic Forest.

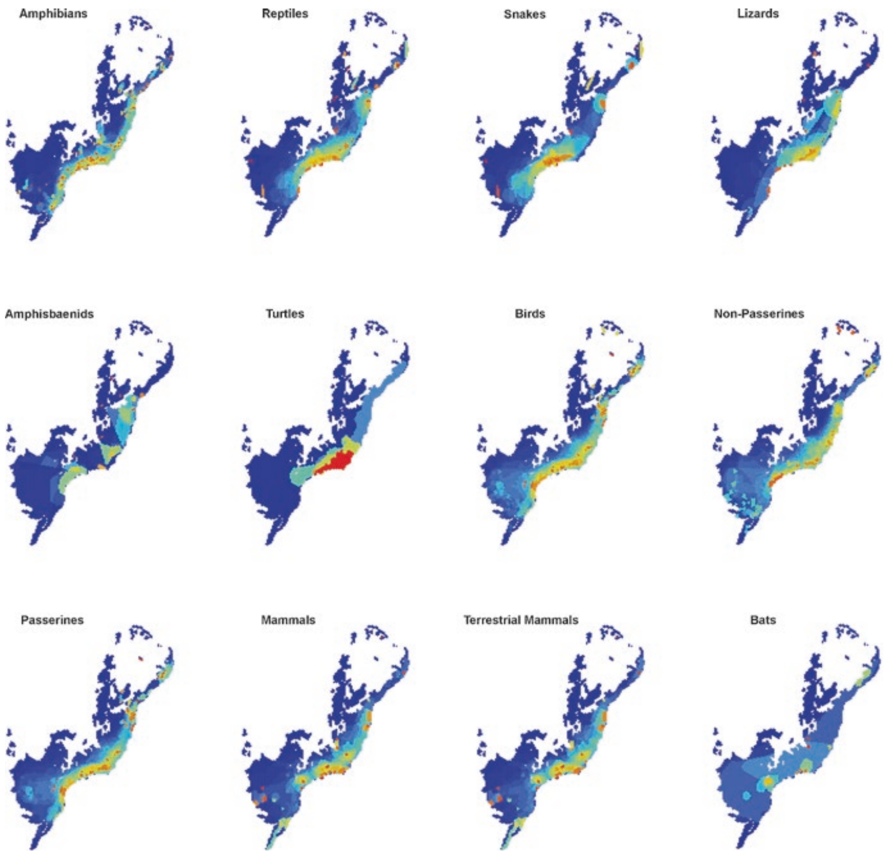

Fig. 9.3 Distribution of observed restricted-range richness for all the groups and subgroups of terrestrial vertebrates in the Atlantic Forest, mapped to a 500 km^2 resolution equal-area (Albers) projection grid. The gradient runs from dark red, which indicates the areas with high values of restricted-range richness, to dark blue which indicates the areas with low values of restricted-range richness

Species yet to be sampled include those inhabiting unsurveyed or hard-to-sample locations or habitat types, such as rainforest canopies or mountain tops (Hortal et al. 2015). Because sampling effort has been concentrated in the center-south of the Atlantic Forest (Figueiredo et al. 2017; Lima et al. 2017; Muylaert et al. 2017; Hasui et al. 2018; Vancine et al. 2018), it is not surprising that many newly described species were based on newly collected individuals from the northeast. For example, the lizard *Placosoma limaverdorum* (Borges-Nojosa et al. 2016), the prehensile-tailed porcupines *Coendou baturitensis* and *C. speratus*, the agouti *Dasyprocta iacki*, and the passerine *Scytalopus gonzagai* (Feijó and Langguth 2013; Pontes et al. 2013; Maurício et al. 2014) were all found in enclaves of the Atlantic Forest surrounded by the Caatinga. Other species have recently been discovered in other poorly sampled environments, such as montane or cloud forests (Whitney et al.

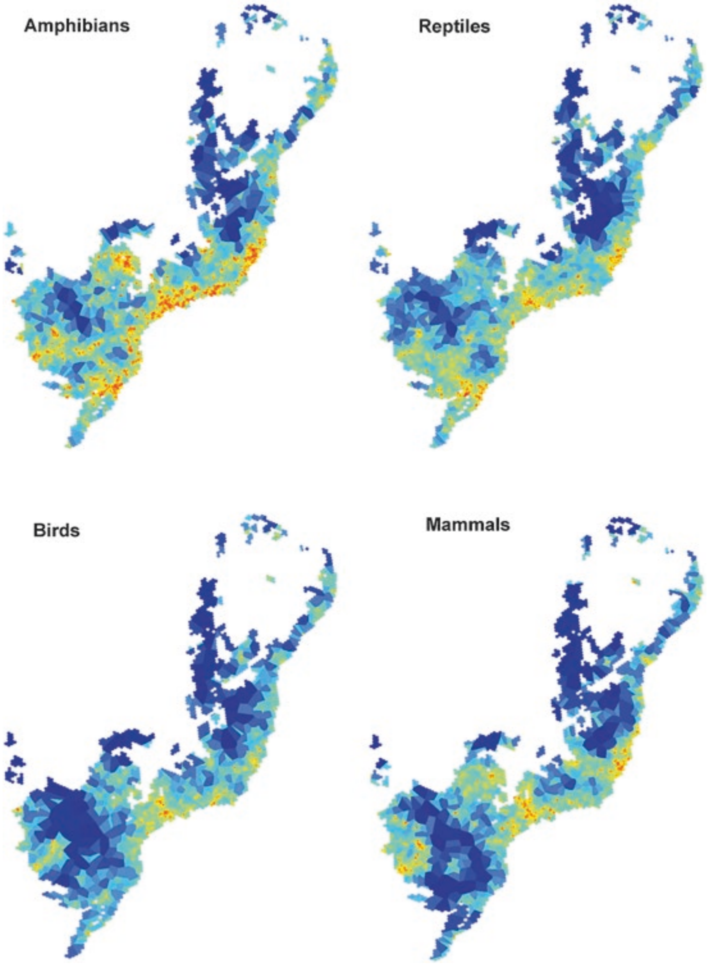

Fig. 9.4 Thiessen polygon networks to represent sampling density. Maps derive from data from the Global Biodiversity Information Facility (GBIF) and from Brazil's SpeciesLink site. The gradient runs from dark red, which indicates the well-sampled areas, to dark blue which indicates the most poorly sampled areas

2010; Brusquetti et al. 2013; Costa et al. 2015; Ribeiro et al. 2015; Bornschein et al. 2016), wetlands (Buzzetti et al. 2013; Quintela et al. 2014, 2017), coastal sandy plains (Tavares et al. 2011; Cardozo et al. 2018), and coastal islands (Barbo et al. 2012, 2016).

Not all new species, however, are from poorly sampled regions. For example, the type localities for the vesper mouse *Calomys cerqueirai* (Bonvicino et al. 2010) and the bat *Dryadonycteris capixaba* (Nogueira et al. 2012) are located in the Rio Doce basin, and the short-tailed opossum *Monodelphis pinocchio* was first identified in the Morro Grande Forest Reserve (Pavan 2015). Two species of the ground-dwelling frogs of the genus *Ischnocnema* were described from individuals collected in the Serra dos Órgãos National Park and Augusto Ruschi Biological Reserve (Taucce et al. 2018). All of these places are in typical and reasonably well-known and studied places within the Atlantic Forest in southeastern Brazil.

The second category of unknown species is more common for small or cryptic species (Riddle et al. 2011), and all are from taxonomic reviews using museum specimens or molecular phylogenies. For instance, two species of snakes of the genus *Atractus* (Passos et al. 2010) and three cryptic species of frogs of the genus *Chiasmocleis* (Forlani et al. 2017) were described based on taxonomic reviews of these genera. The bat species *Lonchophylla peracchii* was split from *Lonchophylla bokermanni* (Dias et al. 2013), while six bird species that were former Atlantic Forest endemic subspecies were recently elevated to the species level (Vale et al. 2018). The rodent species *Delomys altimontanus* and *Rhipidomys itoan* were recently supported by phylogeography and genetics, in addition to traditional morphological analyses (Costa et al. 2011; Gonçalves and Oliveira 2014). Thus, with increased information, new species arise by discovery as well as new by improved analysis.

Lastly, five additional species fit somewhat in both categories, because they were described based on collected specimens that, with additional field work, were recognized as being new species. The bat *Myotis izecksohni* and the dwarf boas *Tropidophis grapiuna* and *T. preciosus* were described after a taxonomic review of *Myotis nigricans* and *Tropidophis paucisquamis* based on recent capture efforts (Moratelli et al. 2011; Curcio et al. 2012). The passerine bird *Cichlocolaptes mazarbarnetti* was split (and included in a distinct genus) from *Philydor novaesi* due to the differences in their behaviors and vocalizations examined during recent field work (Mazar Barnett and Buzzetti 2014). The rat *Drymoreomys albimaculatus*, a very distinctive new genus and species of the tribe Oryzomyini, was described from museum specimens after that inventories on the Atlantic Forest in the state of São Paulo sampled several new specimens (Percequillo et al. 2011).

The Linnean shortfall for Neotropical species is always decreasing over time thanks to the work of taxonomists (Stevens et al. 2020). New species will continue to be described in many places in the world that are already studied, as well as in relatively well-known taxonomic groups. During the last decade, 157 new species of tetrapods were described in the Atlantic Forest, including ten birds (four nonpasserines and six passerines), 14 mammals (three bats and 12 terrestrial mammals), 14 reptiles (one amphisbaenid, six lizards, and seven snakes), and 118 amphibians. The number of endemic species and the evidence of the Linnean shortfall might increase considerably if future taxonomic reviews find that other Atlantic Forest endemic subspecies should be elevated to species level (Vale et al. 2018) or that new species should be described, as expected by the example of the discovery of three yet undescribed new species of the rodent *Phyllomys* (Loss and Leite 2011).

9.4.2 Wallacean Shortfall

The second shortfall refers to the gap of knowledge associated with the geographic distribution of species (Lomolino 2004). The Wallacean shortfall is due to the temporal and spatial variation in surveying efforts (Hortal et al. 2015) that tend to be biased toward more accessible areas (Dennis and Thomas 2000; Vale and Jenkins 2012) and with a greater number of researchers (Rodrigues et al. 2010). These biases may influence perceived and described spatial patterns of species richness (e.g., Nelson et al. 1990; Reddy and Liliana 2003; Bini et al. 2006; Tobler et al. 2007; Werneck et al. 2011).

The Atlantic Forest is the Brazilian ecoregion with the greatest number of biological studies (Jenkins et al. 2015), and access to those data has increased dramatically as online databases become available. We investigated spatial bias in biological surveys of terrestrial vertebrates in the Atlantic Forest, testing whether biological surveys are spatially biased toward access points, such as cities and roads, or high-richness areas.

We gathered occurrence records for all birds ($N = 1661$), mammals ($N = 2502$), reptiles ($N = 3547$), and amphibians ($N = 3883$) within the Atlantic Forest from Global Biodiversity Information Facility (http://www.gbif.org) and SpeciesLink (http://www.splink.org.br). We assumed that if there is a record, there was a biological survey. We compiled records from material sample, literature, and preserved specimen only (excluding mere "observations") and eliminated duplicates and poorly defined geographic coordinates. Using a geographic information system, we generated the same number of randomly distributed points as biological survey sites for each taxon. We then calculated the distance between inventory sites and random points to the nearest access point (roads and cities), using data derived from OpenStreetMap.org (downloaded from MapCruzin, https://mapcruzin.com/free-south-america-arcgis-maps-shapefiles.htm). We also extracted species richness values at each inventory site and random point from richness maps in raster format at a spatial resolution of 10 × 10 km (in an equal area projection – South America Albers Equal Area Conic) derived from Biodiversity Mapping (Jenkins et al. 2013) for birds, mammals, and amphibians, and from Meiri et al. (2017) for reptiles. We compared data from inventory sites and random points using Cohen's d, a measure of effect size defined as the difference between two means divided by a standard deviation for the data (Cohen 1988). Effect size is small when $d \approx 0.2$, medium when $d \approx 0.5$, and large when $d \approx 0.8$ (Cohen 1988). We created a network of Thiessen polygons for each taxon to represent the spatial distribution of sampling effort. In the network, each locality point generates one polygon; the larger the polygon, the lower the survey density (Jenkins et al. 2015).

Biological surveys in the Atlantic Forest tended to be biased toward roads for reptiles, moderately biased toward access points for birds and amphibians, and almost unbiased for mammals (Table 9.3). For amphibians, the analysis suggested the existence of a moderately high survey bias toward high-richness areas, while for birds and mammals, this survey bias is moderate and is moderately low for reptiles

Table 9.3 Cohen's d of the distance to the nearest access point in the distribution of biological surveys and species richness at biological survey sites. The effect was considered small when $d \approx 0.2$, while $d \approx 0.5$ represents a medium effect size, and $d \approx 0.8$ represents a large effect size

				
Distance to nearest city	0.5	0.5	0.6	0.2
Distance to nearest road	0.6	0.7	0.6	0.4
Species richness	0.7	0.3	0.6	0.5

(Table 9.3). Biological surveys tend to be concentrated along the Atlantic coast, mostly in the states of Rio de Janeiro, São Paulo, and Espírito Santo, for all four tetrapod groups (Fig. 9.4). Conversely, large gaps in sampling effort were identified in the interior forests of the northeast and in the meridional plateau in the south, roughly corresponding to four of the bioregions identified by Silva and Casteleti (2003): *Araucaria forests*, *Brejos Nordestinos*, *Diamantina*, and *São Francisco*.

Wallacean shortfall is being reduced through new approaches. For example, the use of increasingly common collaborative databases of species occurrences is providing better information of species occurrence and abundance (e.g., Figueiredo et al. 2017; Lima et al. 2017; Muylaert et al. 2017; Hasui et al. 2018; Vancine et al. 2018). Likewise, citizen science programs result in large volumes of data gathered (Silvertown 2009; Follett and Strezov 2015), often filling sample gaps on a large spatial scale. Even with these initiatives, some species are still hard to find and study, and so due to missing occurrence data, often poorly understood or very rare species suddenly have large range expansions (Passamani et al. 2011; Cerboncini et al. 2014). For example, the bat *Lasiurus ebenus* was described from a single individual on the Ilha do Cardoso State Park, São Paulo (Fazzolari-Correa 1994), and its taxonomic status was questioned. Recently, Cláudio et al. (2018) reported the second record of this species that was collected in Carlos Botelho State Park, also in the state of São Paulo, more than 20 years after its description and 90 km away. This is the most extreme case of Wallacean shortfall for an endemic bat of the Atlantic Forest but is likely to be similar to that for other endemic bats. For example, *Dryadonycteris capixaba* is known from six localities (Rocha et al. 2014), *Myotis izecksohni* is known from seven (Dias et al. 2015), and *Eptesicus taddei* is known from 12 (Bernard et al. 2013). The situation is similar for many species of endemic birds of the Atlantic Forest, and birds are often the best-known group in any region. Using data from the often-used citizen science database WikiAves (www.wikiaves.com.br), 14 species are known from fewer than ten localities (Santos 2019). Eight of those species (*Acrobatornis fonsecai*, *Cichlocolaptes mazarbarnetti*, *Eleoscytalopus psychopompus*, *Glaucis dohrnii*, *Leptodon forbesi*, *Merulaxis stresemanni*, *Philydor novaesi*, and *Scytalopus gonzagai*) are endemic to the forests of the northeast, which reinforces the importance of increasing sampling effort in this region.

Another way to avoid the Wallacean shortfall is using species distribution modeling (SDM). This approach uses occurrence data of a species and environmental variables (such as temperature, precipitation) to describe the distribution (Peterson and Soberón 2012), and it is especially useful to predict distributions of rare or endangered species (Weber et al. 2010; Teixeira et al. 2014). For example, *Lonchophylla peracchii* is known from about 20 localities (Teixeira et al. 2013), and a distribution model for this species indicated where undiscovered populations might occur and guided subsequent sampling expeditions (Teixeira et al. 2014). Indeed, a new population of *L. peracchi* was found (Teixeira et al. 2013). SDM, when developed properly, may provide useful and realistic estimates of distributions of rare and endemic species or, at the very least, indicate future study sites to attempt to fill the gaps (Weber et al. 2010; Teixeira et al. 2014).

9.5 Concluding Remarks

The Atlantic Forest is one of the most diverse ecoregions on Earth, encompassing 8% of all species of tetrapods in the world, ~3% of which are found nowhere else. The Atlantic Forest biota is noteworthy in having an impressive diversity of amphibians (>700 species), with almost 10% of the global total number of amphibian species. It is astonishing that 20% of all Atlantic Forest amphibian species were only described during the past 10 years.

Species richness is greatest at the core of the Atlantic Forest, especially with respect to endemic species. This central, coastal portion of the Atlantic Forest shows a high spatial heterogeneity in topographic conditions, ranging from the sea level to the mountain tops of the Serra do Mar. Apparently, there is a strong, positive association between topography and tetrapod species richness in the Atlantic Forest. Only three groups do not follow this general pattern of richness distribution. Snakes and lizards, due to their ecologic characteristics, showed a different pattern where species richness reaches the greatest values at the contact zones with the dryer savannas, the Cerrado and Caatinga. Bats also follow a distinct, clear pattern of increasing species richness toward the equator.

In addition to the extreme spatial heterogeneity in topography, the core of the Atlantic Forest has also been more extensively studied than other regions in South America and concentrates a disproportionate amount of biological surveys. We found the largest sampling gaps in the interior forests of the northeast and south, where several new species were recently described. Thus, in the future, the Atlantic Forest, already among the most diverse in the world, will soon be found to have even greater species diversity.

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