



Effects of mammal defaunation on natural ecosystem services and human well being throughout the entire Neotropical realm

Juliano André Bogoni^{a,b,*}, Carlos A. Peres^{b,c}, Katia M.P.M.B. Ferraz^a

^a Universidade de São Paulo (USP), Escola Superior de Agricultura “Luiz de Queiroz” (ESALQ), Departamento de Ciências Florestais, Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre (LEMaC), Piracicaba, São Paulo, Brazil

^b School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, Norwich, United Kingdom

^c Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Paraíba, Brazil



ARTICLE INFO

Keywords:

Tropical forest
Defaunation
Ecosystem services
Mammals
Biodiversity crisis
Diseases

ABSTRACT

Mammals embody the apex of ecosystems processes, and their majestic diversity is overwhelmingly threatened in the Neotropical realm. Mammal population declines erode not only several levels of biological diversity, but may also impoverish critical ecosystem services (ES). Based on 2,427 putative baseline mammal assemblages derived from IUCN ranges polygons, we sought to understand, for the first time, the effects of mammal defaunation on natural ecosystem services throughout the entire Neotropical realm. At the assemblage-level, we simulated both stochastic and deterministic regimes of mammal defaunation, examining both diversity indices and classic metrics of ecological networks (e.g. modularity and nestedness). Our results show that ES losses are induced by declines in both taxonomic and functional diversity. Given any defaunation regime, Neotropical provinces undergo levels of ES erosion typically reaching less than a third of all potential network links. Geographic patterns of lost ecosystem services—resulting from simulated and real-world mammal extinctions—indicate that this will detrimentally affect human livelihoods across all major Neotropical provinces. We conclude that the ongoing defaunation process will promote irreversible failures of several mammal-mediated ecosystem processes at varying timescales.

1. Introduction

The Neotropical realm contains myriad endemic species and is the most biodiverse set of ecoregions on Earth. Yet this realm and its biogeographic provinces have been subjected to an unprecedented human-induced biodiversity crisis derived from multifaceted drivers of environmental degradation. The ongoing sixth mass extinction event has erased well over 300 mammal species, which required 3–5 million years of evolution (Davis et al., 2018). Mammal faunas represent the main elements of regional biotas that often succumb to nonrandom population depletion, leading to wholesale local extirpations, particularly in heavily settled parts of the tropics (Dirzo et al., 2014; Bogoni et al., 2018). As a result, the current extinction crisis has exponentially accelerated at local to continental scales compared to background extinction rates (Ceballos et al., 2017).

Several neotropical regions are overshadowed by an imminent mammal diversity collapse in moist humid forests, coastal zones and central plateaus, which have historically been rapidly replaced by

anthropogenic habitats and experienced increasing overhunting pressure since the European colonization of the Americas (Dean, 1996). The concept of defaunation is a legacy of the “empty forest” term coined by Redford (1992) based on seminal studies (Terborgh, 1988; Peres, 1990). This community-level depletion phenomenon is defined primarily in terms of vertebrate species succumbing to demographic or functional extinctions, and downstream effects including the breakdown of key mammal-mediated ecological processes (Redford, 1992). Widespread evidence so far indicates either population depletion or full deletion of large-bodied species prior to replacements by small- to medium-sized species across the Neotropics. This process of density under-compensation increases the abundance of some species, which may partially balance the population decline, extirpation, or absence of potential competitors (Peres and Dolman, 2000), leading to cascading effects that proliferate throughout entire small vertebrate, invertebrate and plant communities (Dirzo et al., 2014).

Mammal population declines—which are often buffered by relatively intact areas—overlap the entire diversity gradient exhibited by

* Corresponding author at: Universidade de São Paulo (USP), Escola Superior de Agricultura “Luiz de Queiroz” (ESALQ), Departamento de Ciências Florestais, Laboratório de Ecologia, Manejo e Conservação de Fauna Silvestre (LEMaC), Piracicaba, São Paulo, Brazil.

E-mail address: bogoni@usp.com (J.A. Bogoni).

<https://doi.org/10.1016/j.ecoser.2020.101173>

Received 18 November 2019; Received in revised form 29 July 2020; Accepted 31 July 2020

Available online 20 August 2020

2212-0416/ © 2020 Elsevier B.V. All rights reserved.

the Neotropics. Based on a pool of ~ 1,550 species of mammals, this gradient of taxonomic diversity ranges from the lowest species richness in southwestern South America (< 50 species) to the highest richness in northern South and Central America (> 200 species) (Ojeda, 2013). Empirical studies have shown that mammalian functional diversity across the Neotropics follows a similar latitudinal pattern (e.g., Oliveira et al., 2016; González-Maya et al., 2017). Functional diversity is undoubtedly an important component of biodiversity because it represents the difference in functional traits between organisms (Tilman, 2001; Májeková et al., 2016), but measures of functional diversity depends on which life history traits are considered (Májeková et al., 2016). Based on morphological, ecological and behavioural criteria (Tilman, 2001), functional diversification resulted from stochastic and evolutionary events that have spawned “eco-spaces”, promoting both inter- and intra-ordinal diversification and impressive ecomorphological convergence (Meredith et al., 2011).

Hence, there is a close relationship between functional diversity and phylogeny, especially phylogenetic diversity (Flynn et al., 2011; Safi et al., 2011; Schweiger et al., 2018). The geography of mammal phylogenetic diversity throughout the Neotropics is also poorly understood. Despite several recent advances, the segmentation of well-known phylogenetic diversity patterns worldwide (e.g., Safi et al., 2011) lacks detail and depends on what phylogenetic data are available. Both phylogenetic and functional diversity embraces many biological aspects that are correlated with ecosystem functioning, due to the interrelated phylogenetic-functional differences among organisms (Tilman, 2001; Schweiger et al., 2018). Evolutionary history constrains species traits within clades (Safi et al. 2011), and these traits—beyond a proxy of species vulnerability to local and regional extinctions (Cardillo et al. 2005, 2008)—impacts their roles in ecosystem functioning. For example, phylogenetically-related ungulate megaherbivores share similar dietary and body size traits that influence many ecological processes, such as herbivory, seed dispersal, seed predation, and ecosystem landscaping (Lacher et al., 2019).

Ensuring well-functioning ecosystems is paramount to provide healthy flows of ecosystem services. Chronic human interferences in natural ecosystems are degrading their ability to provide ecosystem services (Millennium Ecosystem Assessment [MEA], 2003; 2005; Díaz et al., 2013), which are defined as the benefits that people and their well-being obtain from natural ecosystems (MEA 2003, 2005), usually free-of-charge. These include provision, regulation, cultural and support services that directly affect people under the operation of whole ecosystems (MEA, 2003, 2005). Provision services include food production, and availability of water, wood, and fiber. Regulatory regimes include climate buffering, disease regulation, biological and natural damage regulation, water purification, and pollination. Cultural services are linked to ecotourism, education, and cultural heritages and support related services such as soil formation, nutrient cycling and primary production (MEA, 2003, 2005).

The diversity of functional groups—of equivalent species sharing similar traits (Tilman, 2001)—is conceptually important in determining how ecosystem services are assessed (Hooper et al., 2005). Species traits reflect important ecological dimensions (Davidson et al., 2009), and are used to determine direct and indirect ecosystem services (Harrison et al., 2014). Defaunation therefore erodes not only several levels of diversity, but also exerts critical impact on ecosystem functioning and services. However, the extent, geographic distribution and magnitude of how defaunation may affect ecosystem services have not been quantified from local to biogeographic scales across an entire tropical realm.

Accelerated declines in population abundance and elevated extinction risk may degrade critical ecosystem processes mediated by mammals (see Lacher et al., 2019), further justifying more effective and comprehensive conservation action. We therefore seek to understand the effects of mammal defaunation on losses in functional diversity and ecosystem services across the entire Neotropical realm on the basis of

thousands of putative baseline mammal assemblages. Based on the premise that cumulative local extinctions lead to a defaunation footprint of variable spatial scales and intensities across biogeographic gradients, we hypothesize that the worst-case scenarios of defaunation will deplete functional diversity and ecosystem services at magnitude similar to those of contemporary vertebrate population declines (i.e., > 40% according to Ceballos et al., 2017). This may lead to an irreversible collapse in several mammal-mediated ecosystem processes that contribute to human well-being.

2. Methods

2.1. Meta-region of study: The Neotropical realm and its provinces

Several criteria have been used to define the biophysical boundaries of the tropics (Feeley and Stroud, 2018). The Neotropical realm includes all tropical terrestrial ecoregions of the Americas and the entire South American temperate zone, containing 46 biogeographic provinces (Udvardy, 1975). A strict classification of the Neotropical Ecoregion ranges from central Mexico to southern Brazil, including Central America and the Caribbean (Schultz, 2005). Thus, our study region ranged from the northernmost Sierra Madre Occidental (30.5°N) to southernmost South America (Thule do Sul Island, 59.5°S) (Udvardy 1975) (Supplementary Material S1). This geographic realm includes some core features of the tropics, straddling 155 ecoregions (Olson et al., 2001), where (i) the net energy balance is positive and (ii) precipitation seasonality exceeds temperature seasonality (Feeley and Stroud, 2018). The main habitat types within the Neotropical realm are tropical and subtropical moist broadleaf forests, savannas, deserts, coastal forests and mangroves (Olson et al., 2001). For analytical purposes, we adopted a provincial segmentation of the Neotropical realm based on Morrone (2014), resulting in 49 provinces, which is based on biogeographic analyses of all terrestrial plant and animal taxa (Supplementary Material S1).

2.2. Putative Pan-Neotropical mammal assemblages

We systematically searched for all assemblage-wide local mammal studies of all co-existing mammal species across the Neotropics in search engines (e.g. Scopus, Web of Science). This literature search was based on the combination of several keywords such as: “mammals (and all major orders)” AND “distribution (or richness, or inventory/survey)” AND/OR “assemblage(s) (or community (ies) or richness)”. However, these were wholly insufficient in that few surveys can be defined as exhaustive inventories of local faunas, including all terrestrial, arboreal and volant taxa. We therefore extracted 2,427 random putative mammal assemblages within the Neotropical realm (Supporting Information S1) using IUCN range polygons (IUCN, 2018) for all ~ 6000 extant terrestrial mammal species (IUCN, 2018). We further decided to retain some marine species including all nine pinnipeds (*Arctocephalus gazella*, *A. townsendi*, *Callorhinus ursinus*, *Hydrurga leptonyx*, *Leptonychotes weddellii*, *Mirounga angustirostris*, *Otaria flavescens*, *Phoca vitulina*, *Zalophus californianus*) due to their influence on coastal zones (e.g. nutrient transfers from oceanic to terrestrial ecosystems via reproduction and predator–prey relationships) (Cassini, 1999; Trites, 2002).

Simple IUCN ranges polygons usually overestimate mammal occupancy by assuming a 100% range filling, thereby unrealistically inflating local species richness. Relatively few studies are based on data from all broad mammal groupings (i.e. primates, bats and small- to large-bodied species) coexisting at the same localities, thereby addressing both Wallacean (species distributions) and Eltonian (ecological interactions) knowledge deficits (Hortal et al., 2015). This is especially problematic in high-elevation areas (> 1,000 m.a.s.l.), rendering the compilation of a large dataset of real mammal assemblages virtually impossible.

These gaps in biodiversity knowledge can introduce a larger bias than the overfilling of IUCN ranges polygons because most studies are carried out at short distances (< 12.5 km) from main roads and urban centers (Oliveira et al., 2017). Yet continental to global scale studies are usually based on IUCN ranges polygons, which are now a standard data source for all terrestrial mammals in highly cited papers and international databases (e.g., Ceballos and Ehrlich, 2006; Rondinini et al., 2011). We therefore used IUCN-based putative mammal assemblages as a baseline for simulations of contemporary patterns of defaunation. We performed all data compilations using our purpose-created R script (R Core Team, 2018).

2.3. Mammal functional traits

Based on Wilman et al. (2014), Jones et al. (2009), Faurby et al. (2018), and IUCN (2018), we compiled a matrix of non-redundant species functional traits. In doing so, we obtained data on: (1) body mass (adult weight, g); (2) home-range size (ha); (3) species of restricted distributions (binary: < 10 ha); (4) mean dietary energy level (ranked as follows: (i) folivore/grazer < (ii) frugivore/nectivore < (iii) granivore < (iv) insectivore/myrmecophage < (v) carnivore); (5) litter size (absolute N per year); (6) dispersal age (days); (7) habitat breadth (sum of habitat layers); (8) population density (ind/km²); (9) degree of terrestriality (Jones et al., 2009); (10) foraging strata (Jones et al., 2009); and (11) endemism (all species occupying a unique province). For energy levels we weighted the proportion of each major dietary mode of any given species (sourced from Wilman et al., 2014) by their proportional dietary levels (e.g., if an *Alouatta* population consumes 80% leaves and 20% fruits, its trophic level would be 1.2 [i.e. $(0.8 \times 1) + (0.2 \times 2)$). Missing information on species traits was completed with either the mode or mean of the nearest taxonomic level, based on synapomorphy criteria. Remaining missing values were completed via regression models (using the intercepts and slopes) based on an allometric relationship between any trait and species body size (Peters, 1983). However, missing trait cells completed based on either synapomorphy or regression models accounted for only 54 (4.6%) cases. All of these traits were compiled to shed light on the functional redundancy analysis in relation to different defaunation scenarios. However, traits used for the attribution of ecosystem services were restricted to body size and diet, on the basis of a literature review as detailed below (see also Table 1).

2.4. Ecosystem service criteria, matrix multiplication, and bias validation

The critical ecological roles of mammals, focusing on key components of ecosystem functioning, has been recently reviewed (Lacher et al., 2019). Based on the specialized literature—focused on implications of species traits to ecosystem functioning or cultural importance—we therefore attributed the putative presence or absence of 19 previously defined types of ecosystem services (ES; Table 1). For example, according to Stafford et al. (2017) and other studies, the “Food animal protein” ES for traditional Amerindians was defined based on hunting preferences in Mesoamerican and Amazonian forests. The presence or absence of “Insect pest control” ES was based on the Kunz et al. (2011) framework, supported by other empirical evidence (Table 1). Real or potential “Ecotourism” value was based on Harrison et al. (2014) and several other studies (e.g. Salvador et al., 2011; Zhou et al., 2013; Tortato et al., 2017) (Table 1). Two or more literature sources were not mutually exclusive, and were instead combined to form a single putative ES attribution. After compiling the matrix of ecosystem services according to the main species traits (i.e. body size and diet), cultural importance and evidence from the literature, we multiplied the presence-absence matrix of each species per species assemblage by the ES-by-species matrix, thereby deriving a sum of ecosystem services (i.e. the number of species providing each ES) at the assemblage level. We were therefore able to obtain the cumulative

amount of ES per species assemblage across the entire Neotropics. We are aware that we included partly redundant ecosystem services (e.g. phytodemographic dynamics and primary productivity) but we felt this was important to provide a more complete overview of defaunation impacts on ecosystems across the Neotropical realm.

Beyond our own expert opinions grounded on cumulative careers (≈ 72 years) in Neotropical mammalogy, we consulted six specialists (see Acknowledgements) to undertake additional assessments of the attribution of ecosystem services. In doing so, we selected 10 (eco) species of mammals (*Brachyteles* spp., *Dasyprocta azarae*, *Mazama gouazoubira*, *Myotis* spp., *Oligoryzomys* spp., *Panthera onca*, *Pecari tajacu*, *Tapirus terrestris*, *Priodontes maximus*, and *Cerdocyon thous*) and asked each specialist to input the presence (direct and indirect) or absence of each of the 19 ecosystem service for at least one of these 10 (eco)species. We compared our own attribution with those of each specialist, and among them, deriving overestimate or underestimate values for ecosystem services based on a weighted average. Similarly, Barros et al. (2019) also consulted bird specialists to assess an ecosystem service classification based on species traits, but in our approach we examine over a thousand species. Due to this dimensional limitation, we were unable to calibrate the prior trait-based and literature-based ecosystem service attributions, but we measured the level of ecosystem service attribution bias based on the average between over- and underestimations derived from the comparisons across experts.

Based on expert opinions, we verified that our attribution of ecosystem services was overestimated by an average of 2.89% (range = -2.39% to 4.31%). The most overestimated ecosystem services were genetic resources (17.0%), biological control (17.0%), and education (16.0%). On the other hand, other ecosystem services were underestimated, such as ecotourism (-11.0%) and primary production (-9.8%). This also revealed a similar pattern among specialists, with variation in attribution assignment ranging from -3.30% to 4.43% .

2.5. Data analysis

2.5.1. Stochastic and deterministic scenarios of defaunation

Both stochastic and deterministic defaunation scenarios were simulated based on putative baseline assemblages—defined as the “Anthropocene baseline scenario (ABS)” —which represents the current theoretical distribution of mammal faunas throughout the entire Neotropical realm. Based on Dirzo et al. (2014), Pacifici et al. (2017) and Bogoni et al. (2018) we defined stochastic defaunation scenarios, as follows: (1) “Pleistocene extinction scenario (PES)”: by randomly removing from the assemblage matrix 28% of all mammal species based on the median value of Pleistocene mammal extinctions; (2) “Anthropocene extinction scenario (AES)”: by randomly removing 20% of species based on the median of Anthropocene extinctions; (3) “Anthropocene threat scenario (ATS)”: by randomly removing 15% of species based on all threatened species in the Anthropocene; (4) “Climate change scenario (CCS)”: by randomly removing 47% of species, based on all species threatened by climate change; and (5) “Atlantic Forest scenario (AFS)”: since the Atlantic Forest is one of the most threatened Neotropical regions, we randomly reduced the number of mammal species by 71% based on the mean level of mammal defaunation observed across this biome (Table 1).

Deterministic defaunation scenarios were defined as follows: (1) “IUCN threat status scenario (ITS)”: by randomly removing sets of species from mammal assemblages as: (a) 25% of all species classed as “not evaluated (NE)”, “data deficient (DD)”, and “near threatened (NT)”; (b) 50% of all species classed as “Vulnerable (VU)”; (c) 75% of all species classed as “Endangered (EN)”; and (d) 100% of all “Critically endangered (CR)” species; (2) “Body size scenario (BSS)”: by randomly removing 76% of all species larger than 3600 g (mean adult body mass of all large-bodied species); (3) “Home range scenario (HRS)”: by randomly removing 77% of species occupying home ranges larger than 172 ha (mean species home range); and (4) “Energetic level scenario

Table 1

Definitions based on literature sources of real or potential ecosystem services provided by mammal species according to their main functional traits (i.e. body size and diet) and cultural importance across the Neotropical Realm.

Ecosystem Services	Sources	Criteria (direct or indirect)	Trait used ^a
<i>Provision</i>			
Protein acquisition by traditional peoples	Ross 1978; Redford and Robinson 1987; Peres 2001; Cormier 2006; Espinosa et al. 2014; Antunes et al. 2016; Ripple et al. 2016; Stafford et al. 2017; Rodrigues et al. 2019	Hunting preference as a target game species or subsistence need for Amerindians (even with taboos among groups); typically large-bodied species of ungulates, rodents, cingulates and primates. This attribution was based on species ≥ 1 kg for ungulates, rodents, cingulates and primates.	Body size and taxonomic order
Seed predation	Peres et al. 1997; Norconk et al. 1998; Wenny 2000; Hautier et al. 2010; Galetti et al. 2015	Diet based on seed was considered as seed predation; diet of fruits was considered as potential seed predator when species were smaller than 500 g. We adopted this body size threshold because it includes the vast majority of rodents (the main order of seed predators).	Dietary details
Seed dispersal	Peres et al. 1997; Norconk et al. 1998; Wenny 2000; Hautier et al. 2010; Galetti et al. 2015; Lacher et al. 2019	Real or potential seed dispersers based on a diet of fruits independently of consumer specificity (i.e., not only strict frugivores)	Dietary details
Phytodemographic dynamics and timber resources	Peres et al. 1997; Norconk et al. 1998; Wenny 2000; Hautier et al. 2010; Galetti et al. 2015	Based on species diet; Seed predation coupled with seed dispersal; only seed predation; or only seed dispersal. All of these processes regulate phytodemographic changes that affect forest regeneration. Folivory was not included due to the operational definition of predation (i.e. some plant consumers do not necessarily kill them).	Dietary details
Genetic resources	Allem 2000; MEA 2003, 2005; Callier 2019	All species containing genetic resources (including phylogenetic diversity), including to understand the evolution of diseases	Literature
<i>Regulation</i>			
Climate regulation	Peres et al. 1997; Norconk et al. 1998; Wenny 2000; MEA 2003, 2005; Hautier et al. 2010; Galetti et al. 2015; Berzaghi et al. 2018; Lacher et al. 2019	Equivalent to phytodemographic dynamics criteria. Although mammal can also contribute to GHG emissions, the potential mammal-mediated contribution to forest regeneration is paramount to mitigate climate change	Dietary details
Disease control	MEA 2003, 2005; Roemer et al. 2009; Wallach et al. 2015; Lacher et al. 2019	We based this ES attribution on species that prey on potential disease reservoirs	Dietary details
Insect pest control	MEA 2003, 2005; Kunz et al. 2011; Lacher et al. 2019; Rodrigues et al. 2019	Diet of invertebrates contributing to the regulation of insect populations that damage crops	Dietary details
Biological control	MEA 2003, 2005; Roemer et al. 2009; Wallach et al. 2015; Peres et al. 1997; Norconk et al. 1998; Wenny 2000; Hautier et al. 2010; Galetti et al. 2015; Berzaghi et al. 2018; Lacher et al. 2019	All species, as predators or prey, or for detritivores foodweb, or as a competent disease reservoir, or as seed predators, or seed dispersers (i.e., all ecological process)	Literature
Recovery from natural disasters	Sieg 1987; MEA 2003, 2005; Shiels et al. 2015; Seidensticker 2016	All species contributing to ecosystem resilience in the aftermath of perturbation. For example, forest regeneration via seed dispersal and the population control of species that benefit from perturbations	Literature
Pollination	MEA 2003, 2005; Kremen 2005; Kunz et al. 2011; Lacher et al. 2019	Diet of nectar or pollen	Dietary details
<i>Cultural</i>			
Ecotourism	MEA 2003, 2005; Harrison et al. 2014; Salvador et al. 2011; Zhou et al. 2013; Tortato et al. 2017	Real or potential, typically species larger than 44 kg (charismatic megafauna)	Body size
Ethnocultural identity	MEA 2003, 2005; Cormier 2006; Busatta 2007; Alves et al. 2012;	Sacred animals for Amerindians and/or species used for subsistence by traditional peoples. This attribution was similar to Protein acquisition by traditional peoples but included records of animals considered to be sacred	Literature
Aesthetic	MEA 2003, 2005; Harrison et al. 2014	All species effectively or potentially contributing to natural aesthetic values	Literature
Education	MEA 2003, 2005; Ulbrich et al. 2010	All species having real or potential contribution to educational values	Literature
<i>Support</i>			
Soil formation	Reichman and Smith 1990; Davidson et al. 2012; Harrison et al. 2014; Haussmann 2017; Lacher et al. 2019; Rodrigues et al. 2019	Fossorial or burrowing habit, excluding aspect of soil fertility and/or erosion (considered as a (de)service)	Literature
Oxygen production	Peres et al. 1997; Norconk et al. 1998; Wenny 2000; Hautier et al. 2010; Galetti et al. 2015; Berzaghi et al. 2018	Equivalent to phytodemographic dynamics criteria aforementioned	Dietary details
Nutrient cycling	MEA 2003, 2005; Berzaghi et al. 2018; Lacher et al. 2019; Rodrigues et al. 2019; Bogoni et al. 2019	All species contributing to nutrient cycling throughout the foodweb (including detritivore foodwebs)	Literature
Primary productivity	Peres et al. 1997; Norconk et al. 1998; Wenny 2000; MEA 2003, 2005; Hautier et al. 2010; Galetti et al. 2015	Equivalent to aforementioned phytodemographic dynamics criteria	Dietary details

^a Some ES were based only on evidence from the specialized literature.

(ELS)”: by randomly removing 78% of species operating at high trophic levels (> 2.73: mean energetic level) (Table 1). Defaunation rates for deterministic BSS, HRS and ELS scenarios were calculated according to the distribution of functional groups based on observed defaunation

rates (see Bogoni et al., 2018). Based on the stochastic and deterministic scenarios, we were able to make comparisons between random defaunation and “real-world” scenarios (i.e., trait-prone-based defaunation).

2.5.2. Functional redundancy responses to defaunation

We explored the taxonomic diversity (T_{Div}) for putative baseline mammal assemblages and their erosion under different defaunation regimes. We also derived the functional redundancy (F_{Red}), a measure obtained from the difference between species diversity and Rao's quadratic entropy based on their functional dissimilarity (Ricotta et al., 2016). Maintaining ecosystem processes under any scenario of species loss requires that some species perform similar functions (Villéger et al., 2008). Species similarity therefore implies a lesser impact on ecosystem processes, which is usually known as functional redundancy (F_{Red}) (Naeem, 1998). We examined differences in diversity variation observed under the stochastic and deterministic scenarios in relation to the expected baseline (ABS) via χ^2 tests (Pearson, 1900). To explore and compute functional redundancy, we used an R code (R Core Team, 2018) based on the SYNCSA packages (Debastiani and Pillar, 2012).

2.5.3. Defaunation effects on ecosystem services

Given the mammal assemblages under the baseline and each defaunation scenario, we used ecological bipartite networks to examine matrices of adjacency of ecosystem services at the assemblage-level, obtained from each scenario and set of species traits (Boccaletti et al., 2006). In these terms, a vertex represents the number of species in each assemblage connected to any ecosystem service they provide. For assemblage-ES networks, we obtained the following metrics: (i) assemblage degree (AS_d); (ii) ecosystem services degree (ES_d); (iii) connectance (C); (iv) nestedness (N); and (v) modularity (M).

The average degree (xAS_d and xES_d) describes the mean number of interactions between species and their putative ES per assemblage in the network (Boccaletti et al., 2006). The AS_d for each assemblage and ES_d for each ES represents the quantitative ES lost under each defaunation scenario. Modularity (M) quantifies the tendency of the nodes (species per assemblage and service) to form groups of vertices that are more connected to each other than to other components of the network. Connectance (C) represents the proportion of observed interactions in relation to the total number of possible interactions (Boccaletti et al., 2006). Nestedness (N, based on NODF criteria) indicates a hierarchical pattern of interactions, in which interactions of less connected species/ecosystem services form a subset of the interactions of the most connected, representing a structural fitting (Almeida-Neto et al., 2008). Thus, nestedness can indicate that the richest and compositionally more redundant assemblages can retain a large fraction of their original ES even under defaunation, including more impoverished or more defaunated assemblages that are less functionally redundant. We compared these metrics between the baseline assemblages and their respective defaunation scenarios, whereby any numerical change suggests either a loss or gain in robustness or stability of the network of services provided by subsets of species.

For modularity (M) and nestedness (N), we used a null model approach (Gotelli and Graves, 1996) to test statistical significance levels. We created 1000 matrices by randomizing all ecosystem services at the assemblage level based on a probability matrix, considering the minimum and maximum empirical number of ecosystem services per assemblage (null model 2 of Bascompte et al., 2003). For each null matrix, we calculated the modularity (M) and nestedness (N), thereby creating distributions with which we compared observed values for each scenario. Defaunation scenarios in which M and N values decreased outside the 95% confidence intervals of null distributions were considered significant (Bascompte et al., 2003). Presumed decreases in modularity indicate the non-random loss of network cohesion. Presumed decreases in nestedness may numerically predict declines in the overall amount of ES provided, but presumed increases in nestedness can indicate inequality in ES distribution among species. To explore network formalities and compute their metrics, we used an R code (R Core Team, 2018) based on the *bipartite* package (Dormann et al., 2008).

2.5.4. Spatial patterns

To interpolate assemblage-level diversity indices for the entire Neotropical realm, we initially used the Moran index (M) to assess the spatial autocorrelation of mammal species richness (Legendre et al., 2015). Since a spatial autocorrelation of richness was detected [$Moran_{(obs)} = 0.17$; $Moran_{(exp)} = -0.01$; $p < 0.05$], we used a kriging approach to interpolate the baseline, the worst-case, and the mean stochastic and deterministic scenarios into final diversity maps (Cressie, 1993; Pebesma, 2004; Biondi, 2013). Kriging, which is frequently used for optimal data interpolation, is an inverse distance weighting (IDW) geostatistical method that requires a semivariogram model to describe the spatial autocorrelation pattern of any particular variable (Pebesma, 2004; Biondi, 2013). We also used this workflow to geographically interpolate the mean loss of ES under the worst-case, stochastic, and deterministic scenarios.

3. Results

3.1. Overall trends in data compilation

We compiled data on 1,153 mammal species distributed across 2,427 assemblages encompassing ~ 20.4 million km^2 , which represented 165,633 presence records (or 5.92%) within a full matrix of 2,798,331 cells. Across the 49 Neotropical provinces, there were 49.5 (± 56.8) assemblages per province, ranging from two (Bahama province: 5,443 km^2) to 238 (Cerrado province: $\sim 2M$ km^2). This resulted in a ratio of 0.012 mammal assemblages per 100 km^2 spaced apart by a mean distance of 3,182 km ($\pm 1,996$ km ; range = 1.4–11,969 km) (Supporting Information S1).

3.2. Mammal diversity under assemblage-scale defaunation regimes

The baseline scenario (ABS) showed a mean taxonomic diversity of 68.2 (± 35.0) species, ranging from one (Bahama province) to over 100 species within Amazonian provinces (e.g., Madeira, Xingú-Tapajós, Roraima, Imerí, Pantepui, Guianan Lowlands, Napo; Fig. 1). As predicted under the stochastic defaunation scenarios—based on random removals of 15% to 71% of all species—taxonomic diversity declined in equal proportion in comparison with the baseline scenario. Taxonomic diversity on average decreased by 27.2% (from 8.1 to 59.0%) compared to the baseline. In particular, AFS was the worst-case defaunation scenario, showing a mean reduction of 45.9 species compared to our baseline. Under this future scenario subjected to several human-induced threats, the estimated taxonomic diversity across all 2,427 assemblages was 18.9 (± 10.6) species, and all provinces were projected to retain fewer than 40 mammal species (Fig. 1). All defaunation scenarios were expected to yield a significantly lower taxonomic diversity (T_{Div}) compared to our baseline scenario [$\chi^2 = 23.8$; $df = 8$; $p < 0.01$].

Beyond the worst-case scenario (71% of defaunation), functional redundancy changes were most numerically pervasive under the stochastic scenarios ($F_{Red(baseline)} = 0.603$; $F_{Red(stoch.)} = 0.587$; Fig. 1; Supplementary Material S3). Changes in functional redundancy (F_{Red}) were not significantly different compared to that expected under the baseline scenario [$\chi^2 = 0.01$; $df = 8$; $p = 1.00$].

3.3. Effects of defaunation on ecosystems services

Defaunation not only eroded the overall taxonomic and functional diversity, but also led to a non-random decline in ecosystem service flows. Based on the baseline scenario (ABS), ongoing depletion of mammal faunas can completely eliminate some ecosystem services, given the resulting putative assemblages. Scaling the erosion of ES, our results show decreases ranging from 4% of assemblage degree (i.e., number of species in each assemblage providing each ecosystem services) under the deterministic ITS scenario to 71% under the stochastic

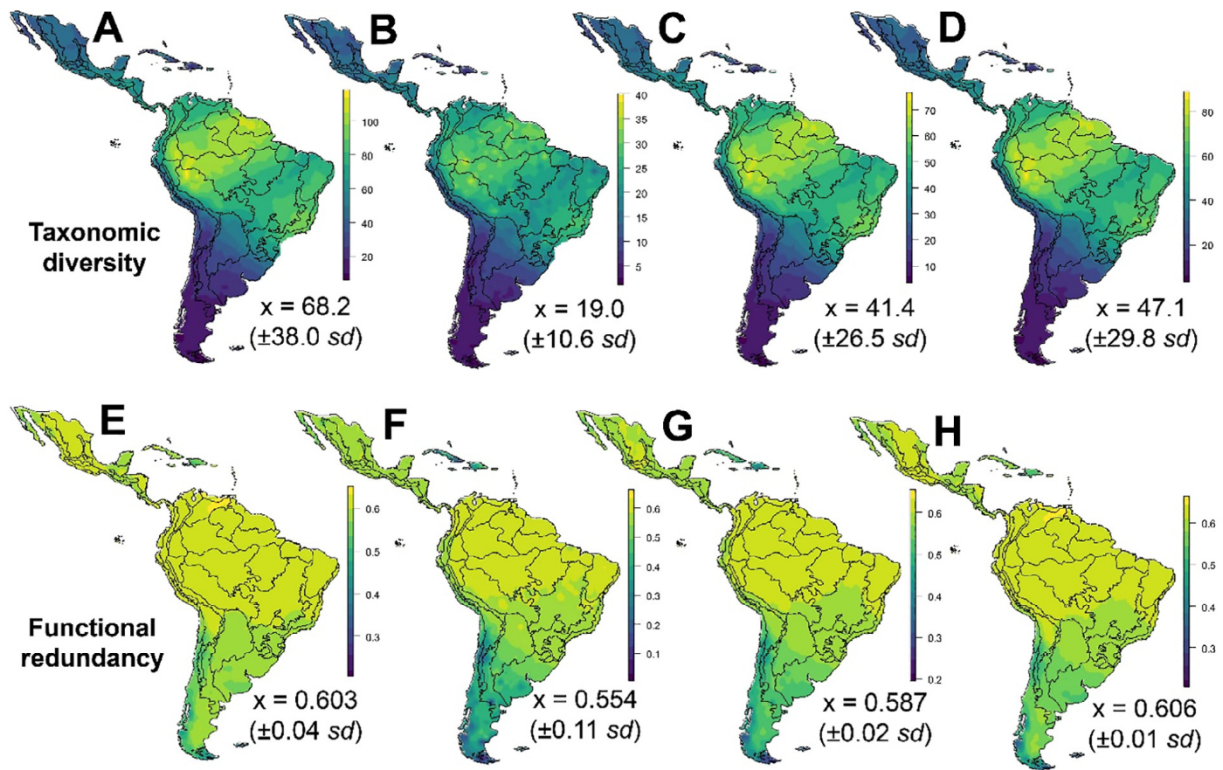


Fig. 1. Taxonomic diversity and functional redundancy of mammal faunas across the Neotropical realm and its provinces, following the criteria: (i) Diversity based on 2,427 putative mammal assemblages extracted at random from IUCN range polygons (ABS scenario); (ii) The same 2,427 assemblages experiencing a 71% defaunation rate (AFS scenario); (iii) Average diversity under stochastic defaunation regimes; and (iv) Average diversity under deterministic defaunation regimes. The maps, from A to D and from E to H have different scales, and respectively represent, for taxonomic diversity and functional redundancy, the baseline (A and E), worst-case scenario (B and F), average of stochastic scenarios (C and G), and average of deterministic scenarios (D and H).

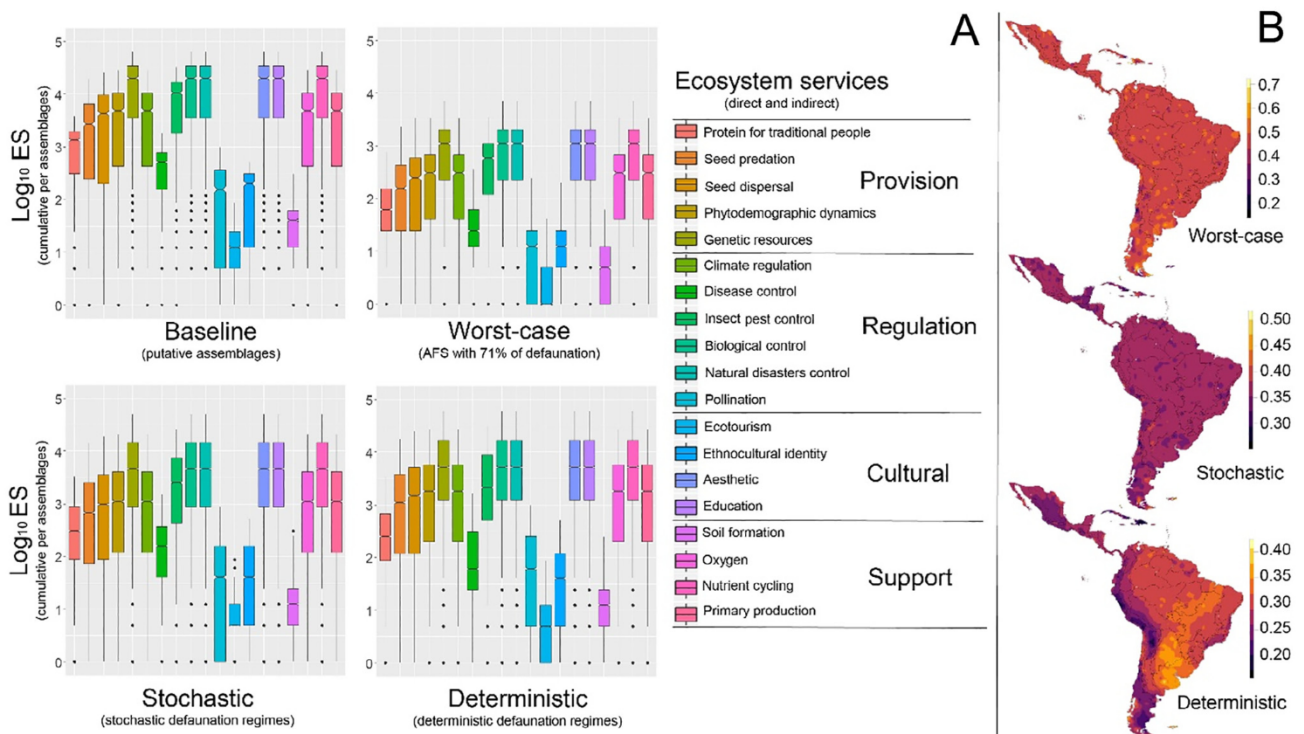


Fig. 2. (A) Putative ecosystem services (ES) provided by mammals throughout the Neotropical realm considering the baseline state (ABS), the worst-case defaunation scenario (AFS) and the average between stochastic and deterministic regimes of defaunation; and (B) Ratio of spatial loss of ES under the worst-case, stochastic and deterministic defaunation regimes. Note the different scale in losses of ecosystem services in panel B.

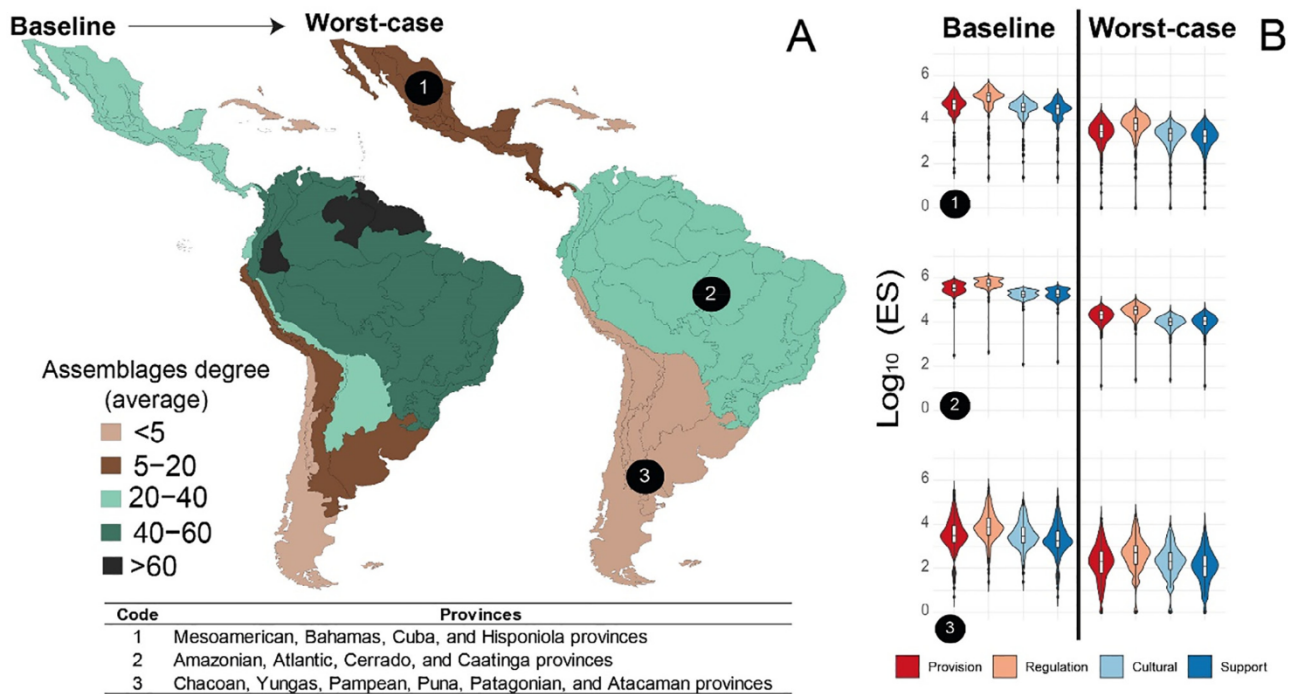


Fig. 3. (A) Change in assemblage degree revealing the magnitude of ES losses across Neotropical provinces based on the baseline (ABS) and worst-case defaunation scenarios (AFS). Assemblage degree (average) represents the average number of links between mammal species represented in any given assemblage and 19 types of ecosystem services. (B) Ecosystem services loss projected by the worst-case scenario (AFS) compared to the baseline (ABS) across all major Neotropical regions and provinces.

AFS scenario. Under the deterministic scenario, the main ES affected across different defaunation regimes were ecotourism, soil formation, disease control and protein acquisition by traditional people, all of which declined by over 40% (Fig. 2). Under the worst-case scenario (AFS), Neotropical provinces would lose ES at approximately similar rates, but provinces characterized by naturally low diversity (e.g., Pampean, Monte, Puna, Patagonian, and Atacaman) were most penalized (Fig. 3). In absolute terms, these results represent a loss of 1,200,332 links (71.2%) within the overall baseline assemblage-scale ES network. Our defaunation scenarios predicted a depletion rate ranging from 64,565 (3.8%; ITS scenario) to > 1 million links in the overall fabric of ES × assemblage networks. The main ecosystem services eroded under different defaunation scenarios were ecotourism (43.4%), soil formation (39.8%), disease control (39.6%), protein acquisition for subsistence (38.0%) and ethnocultural identity (37.3%), whose losses under the deterministic defaunation regime ranged from 38.9% to 53.0% compared to the baseline.

Changes in network structure confirmed the aforementioned patterns. Our results derived from the deterministic scenarios reveal a loss of taxonomic diversity of 27.2%, and a mean functional redundancy of 1.32%, amounting to a mean loss of 505,188.3 links (ca. 30%) across the baseline network or 208.2 links per assemblage. Among the network metrics, we highlight the reductions in AS_d and ES_d , which ranged from 26 (3.7%) to 492 (70.9%) and from 3,598 (4.1%) to 63,375 (71.4%), respectively, in relation to baseline assemblages. Overall nestedness was also heavily affected, increasing from 1.08 (2.1%) to 28.47 (57.2%) across different defaunation scenarios compared to the baseline, mainly in the CCS and AFS (stochastic), and BSS, HRS, and ELS (deterministic) scenarios (Supplementary Material S2). Null models showed that, across all scenarios examined here, network modularity was statistically lower than expected by chance [$M_{average_scenarios} = 0.036$; $M_{average_null} = 0.069$; $p < 0.01$]. Finally, variation in nestedness across all scenarios, was significantly different from that expected under a null distribution [$N_{average_scenarios} = 62.74$; $N_{average_null} = 65.70$; $p < 0.01$] (Supplementary Material S2).

4. Discussion

A paramount challenge in how conservation ecology can inform the emergent science of ecosystem services is to quantitatively understand the effects of biodiversity loss on human well-being. Recent empirical studies have shown the overwhelming simplification of mammal faunas worldwide, depleting perhaps the most charismatic biotic component of tropical environments, often undermining their ecosystem functions and services (e.g., Dirzo et al., 2014; Peres et al., 2016). Even accounting for the legacy of the Pleistocene overkill (Surovell et al., 2016), mammals still represent the largest surviving elements of Earth’s terrestrial megafauna, performing several critical functions on local ecosystems (Lacher et al., 2019). Yet European colonization of the Americas further dramatically eroded tropical forest biotas worldwide, including the stark population collapse of pre-European peoples (Koch et al., 2019). Virtually all Nearctic and Neotropical biomes subsequently succumbed to further biodiversity declines over the last two centuries, due to a wide range of human-induced catalysts following modern agropastoral frontier expansion. Based on a growing body of empirical evidence, dwindling population sizes and range shrinkages of key elements of vertebrate faunas amount to a colossal anthropogenic loss of both biodiversity and all attendant ecosystem services (Ceballos et al., 2017).

Recent studies indicate much empirical and experimental evidence that species richness boosts community biomass production and ecosystem stability (Duffy et al., 2017). Our estimates support a growing body of evidence on the positive nonlinear relationship between the biotic integrity and functioning of ecosystems (Tilman, 1996; Chapin et al., 2000). Scenarios of defaunation reduced ES per assemblage by an average of 33.5%. This ES reduction could be seen as relatively modest compared to rates of > 40% contemporary vertebrate population declines (Ceballos et al., 2017), but this is far from trivial considering the scale of our dataset. We collated data on > 2,400 assemblages containing over 1,100 mammal species and 11 species traits. A mean 33.5% ES loss per assemblage can profoundly diminish local to regional

scale ecological functions.

We highlight that the loss of ESs is modest compared to the loss of network assemblage-ES links, apparently because it was buffered by the redundancy in ES provided by different species. For example, any species operating as seed predators or seed dispersers contributed equally to phytodemographic dynamics. Our results of the functional approach confirm this pattern, showing novel responses in the functional redundancy metrics used. Functional redundancy (F_{Red}) actually decreased slightly (1.32%) under the defaunation scenarios we tested. Given our presence-absence data, this slight decrease in F_{Red} indicates that the remaining extant species are more dissimilar compared to the baseline. This lower variation indicates an increase in the mean distance in multidimensional trait space of individual species to the centroid of all species and a decrease in species similarity (i.e., a loss of “backup”). However, defaunation amounted to a reduction in space overlap in all cases. These results imply that the apparently weak alteration in functional metrics per se masks the large loss and displacement in the functional space of assemblages succumbing to local extinctions.

These estimates do not take into account unpaid extinction debts. Local mammal extinctions have occurred at alarming rates, yet their detection has been limited in some cases, underestimating the degree to which a biota is actually threatened (Ceballos et al., 2017). Population sizes have critical roles in ecosystem functioning, which have mechanistic proprieties that can be disrupted at different scales depending on biotic integrity (Ceballos et al., 2017). Co-extinctions can also potentialize the negative effects on ecosystem functioning and services (Strona and Bradshaw, 2018; Bogoni et al., 2019), highlighting the need to understand the role of associated species in biodiversity-ecosystem function relationships.

From a species trait perspective, deterministic scenarios are more plausible given that some traits predispose species to local extinctions (Cardillo et al., 2005; 2008; Pimm et al., 2014), and current extinction rates are 114 times higher than the background rate (Ceballos et al., 2015). Conversely, stochastic scenarios are conceptually less plausible from a trait perspective. Some 9,826 local extinctions of medium- to large-bodied mammals have been empirically observed throughout the Atlantic Forest biome of South America (Bogoni et al., 2018). Given that this biome represents only 6.4% of the total continental area examined in this study, population losses could proportionally exceed 153,000 local extinctions, or an average of 63.1 per mammal assemblage.

A growing body of evidence has pointed to the ecological costs of mammal defaunation (Kurten, 2013; Carvalho et al., 2016; McConkey and O’Farrill, 2016; Peres et al., 2016). These ecosystem-level consequences are aggravated because extinction risk in many mammal populations is induced by a combination of several factors, including small geographic range, low population density, slow life histories, delayed weaning age, and large body size (Cardillo et al., 2005; 2008; Davidson et al., 2009). Human overexploitation exerts further detrimental effects that accelerate population declines and local extinctions (Cardinale et al., 2012; Dirzo et al., 2014). As a key driver of mammal defaunation in tropical forest regions, this includes a long and recurrent history of overhunting, habitat conversion and fragmentation, or the synergistic combination of both (e.g., Peres, 2001).

With the exception of pollination, which in any case is infrequently provided by neotropical mammals, all ES types showed mean depletion rates > 30%. Ecotourism, although underestimated by 11%, is one of the most meaningful ecosystem services related to large-bodied vertebrates, according to expert opinion and recent growth in wildlife tourism in South America. For instance, jaguar ecotourism alone represents a gross annual income of nearly US\$7 million in land-use revenues of a relatively small portion (81,000 ha) of the Brazilian Pantanal wetlands (Tortato et al., 2017), which is three-fold greater than the value of the staple economy based on traditional cattle ranching. Yet the currently realized value of mammal ecotourism

throughout the Neotropics is still a very small fraction of the future potential value of this industry, at least at sites where relatively intact mammal assemblages can be protected.

Predators control prey populations, scavengers remove carrion from the landscape, and large-bodied fossorial mammals create physical changes in the abiotic environment, all of which render biophysical resources more available for other species, thereby contributing to ecosystem health (Machicote et al., 2004; Barry et al., 2018). Large burrows also promote soil translocation, aeration, and exposure (Hausmann, 2017; Rodrigues et al., 2019), favouring soil formation. Disease control is a density-dependent process that at non-equilibrium can lead to increased prevalence of infectious diseases in humans (Levi et al., 2012; Guterres and Lemos, 2018). Ethnocultural identity and availability of animal protein from wild game for traditional peoples are generally co-eroded with biodiversity loss (Pretty et al. 2009).

Our network metrics confirmed our estimates of defaunation-induced ES erosion. For instance, an increase in nestedness under any defaunation scenario compared to the background baseline indicates that a small group of species provides a disproportionately large number of ES, whereas a large number of species provides only one or a few ES, which may threaten ecosystem stability and functioning. Moreover, overall nestedness was higher than expected by chance in the worst-case AFS and HRS scenarios of ES_d erosion. This suggests a disproportionate role of a small group of ES-dominant species compared to a dense core of interactions to which the rest of the assemblage is linked (i.e. a highly heterogeneous distribution in the number of ES-species interactions). Nestedness organizes any given assemblage in a highly asymmetrical way, with most specialist species being able to interact only with the most generalist ES (Bascompte et al., 2003).

In particular, ES_d—which describes the mean number of species interactions per assemblage in relation to putative ecosystem services—was one of the most degraded network metrics examined here. This further confirms that local extinctions lead to a quantitative loss in ES. However, this form of ES loss was substantially buffered by the functional redundancy in the network. Ecological similarity among species lessens the impact on ecosystem processes, often serving as a backup (Naeem, 1998). Functional redundancy ranges from 0.0 to 1.0 and our results showed a maximal divergence of only 0.054 between different defaunation scenarios, suggesting a persistent eco-similarity among mammal species but failing to ensure the quantitative and qualitative functionality of ecosystems.

Therefore, ES losses were most strongly associated with declines in taxonomic diversity. In many cases, assemblage functional space could not be maintained if a high proportion of ecologically similar sympatric congeners were deleted. For instance, a loss of 1.37% in functional redundancy in this analysis corresponded to a loss of 30% in assemblage-scale ES. Typically, the most species-rich putative assemblages contained many species of bats and rodents (69.8% of all 1,147 mammal species examined here) with a large functional trait overlap. This may explain the significant discrepancy between loss in taxonomic diversity and loss in ES. By simulating the effects of defaunation at a pan-neotropical scale, we were able to show that the most penalized biogeographic provinces contain high rates of unique species but the most species-poor assemblages (see Fig. 3).

Among the 19 ESs considered here, we highlight the debilitation of seed dispersal capacity under post-extinction scenarios. Under deterministic defaunation regimes, mean loss in seed dispersal reaches one-quarter of the overall matrix, representing 20,380 deleted interactions across the Neotropical realm (or 18,575 accounting for the 8.5% overestimation of this service). Seed dispersal is a particularly critical ES provided by (largely midsized to large) mammals because over 90% of all plant species in Neotropical forests are vertebrate-dispersed (Howe and Smallwood, 1982). Although operational effects of seed dispersal and seed predation remains poorly understood in much of the tropics, the classic dichotomy between dispersal agents seed disperser oversimplifies the complexity of plant-animal interactions (Norconk

et al., 1998). Yet, both processes ensure appropriate forest regeneration, phytodemographic dynamics, and result in a series of important trophic cascades structuring ecosystem patterns and processes (Janzen, 1971; Peres et al., 2016). Our findings also showed that the connectance in assemblage-ES networks remained both high and stable, ensuring a “rescue effect” induced by species redundancy in their functional roles in ecosystems. However, we reinforce that failures in ES provisioning resulting from defaunation were quantitatively meaningful. For example, if at least 19 species, each performing a type of ecosystem service (i.e. 19), the binary network connectance remains high. Likewise, modularity did not indicate a tendency of the assemblage-ES nodes to form groups of vertices that are more connected to each other than to other components of the network, indicating that the species ‘backup’ is only discontinued once the last species performing a single ES is driven to local extinction. We further reinforce that the modern collapse of mammal faunas across the Neotropical realm implies in more quantitative, rather than qualitative, consequences as long as any functional redundancy continues to operate. Moreover, we highlight that ~ 82% of all assessed mammal species are small-bodied (< 1000 g), and that speciose clades typically accommodate much infra-ordinal sympatric diversity (e.g. rodents and bats) promoting functional redundancy and stabilizing changes in the network metrics as long as defaunation rates are not severe.

Further, we recognize that ES attributions according to species traits can often be biased. We showed that there was meaningful variation in ecosystem service attribution among mammalogists. However, the net balance between overestimates and underestimates was ca. 3%. Some ecosystem services seem to be more overestimation-prone (e.g. education, ethnocultural identity, and biological control) while others were underestimated (e.g. soil formation, seed predation, and ecotourism). Yet our measures of ecosystem services provided by mammals throughout the Neotropical realm were largely reliable, and the biases we quantified did not greatly affect comparisons between defaunation regimes. For example, correcting for the 2.89% mismatch in ES_d, we still showed a loss from 3,494 to 61,543 average links compared to the baseline. Although studies of ecosystem services based on species traits are now increasingly widespread, there are limitations in this approach calling for a more encompassing synthesis (Tilman, 2001; Balvanera et al., 2014; Harrison et al., 2014). Given that both baseline and different defaunation scenarios were built under the same criteria of ES attribution, our scenario comparisons are entirely reasonable. Another issue we highlight is the partial redundancy among some ecosystem services considered here, but this does not affect our estimates of ecosystem service losses induced by defaunation across the Neotropics. Moreover, we emphasize that further experimental studies could, therefore, help elucidate predictions of how different patterns of biodiversity loss will degrade ecosystem services.

5. Conclusions

In integrating our estimates with a wider body of empirical evidence, we can conclude that many ecosystem services are now threatened due to massive diversity loss. We emphasize that human well-being depends heavily on biodiversity conservation at varying spatio-temporal scales, and that the local effects of biodiversity loss are propagated at regional to continental scales. The central hypothesis we posed here has therefore been endorsed because the loss of large-bodied species, and/or consumers at high trophic levels resulted in the erosion of ecosystem services that on average involved over 30,000 (34%) network links. In the medium term, this ongoing defaunation process could promote irreversible failures of several mammal-mediated ecosystem processes that ensure human well-being.

In exploring the role of local extinctions, we showed that even small changes in functional indices driven by vertebrate defaunation were meaningful when aggregated at larger scales of ecosystem functioning. However, compositional and patterns of contemporary defaunation

experienced throughout the entire Neotropical realm remain unclear. However, we stress that perpetuating the integrity of complex systems will depend on our collective effort to pursue effective conservation strategies that encompass the taxonomic, functional and phylogenetic diversity of life at all spatial scales. This includes ensuring the persistence of increasingly embattled large protected areas and eradicating overhunting.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We sincerely thank all researchers who obtained and organized the datasets compiled in this study. We thank Adriano Chiarello, Arnaldo Desbiez, Marcelo Magioli, Maurício Graipel, Rodrigo Massara, and Ronaldo Morato for their expert opinion about species-based ecosystem service attributions. We thank two anonymous reviewers for important contribution on our manuscript.

Funding

JAB is supported by the São Paulo Research Foundation (FAPESP) postdoctoral fellowship grants 2018-05970-1 and 2019-11901-5. KMPMBF is funded by research grant (308632/2018-4) from the Conselho Nacional de Pesquisa e Desenvolvimento Científico e Tecnológico (CNPq).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoser.2020.101173>.

References

- Allem, A.C., 2000. The terms genetic resource, biological resource, and biodiversity examined. *Environmentalist* 20, 335–341.
- Almeida-Neto, M., Guimarães, P., Guimarães Jr., P.R., Loyola, R.D., Ulrich, W., 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. *Oikos* 117, 1227–1239.
- Alves, R.R., Rosa, I.L., Neto, N.A.L., Voeks, R., 2012. Animals for the gods: magical and religious faunal use and trade in Brazil. *Hum Ecol* 40, 751–780.
- Antunes, A.P., Fewster, R.M., Venticinque, E.M., Peres, C.A., Levi, T., Rohe, F., Shepard Jr., G.H., 2016. Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Sci. Adv.* 2(2), e1600936.
- Barry, J.M., Elbroch, L.M., Aiello-Lammens, M.E., Sarno, R.J., et al., 2018. Pumas as ecosystem engineers: ungulate carcasses support beetle assemblages in the Greater Yellowstone Ecosystem. *Oecology* 189, 577–586. <https://doi.org/10.1007/s00442-018-4315-z>.
- Balvanera, P., Siddique, I., Dee, L., Paquette, A., et al., 2014. Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. *BioScience* 64(1), 49–57.
- Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant – animal mutualistic networks. *Proc. Nat. Acad. Sci.* 100(16), 9383–9387. <https://doi.org/10.1073/pnas.1633576100>.
- Barros, F.M., Peres, C.A., Pizo, M.A., Ribeiro, M.C., 2019. Divergent flows of avian-mediated ecosystem services across forest-matrix interfaces in human-modified landscapes. *Land. Ecol.* 34, 879–894.
- Berzagli, F., Verbeeck, H., Nielsen, M.R., Doughty, C.E., et al., 2018. Assessing the role of megafauna in tropical forest ecosystems and biogeochemical cycles – the potential of vegetation models. *Ecography* 41, 1–21.
- Biondi, F., 2013. Space-time kriging extension of precipitation variability at 12 Km spacing from tree-ring chronologies and its implications for drought analysis. *Hydrol. Earth Syst. Sci. Discuss.* 10, 4301–4335.
- Boccaletti, S., Latora, V., Moreno, Y., Chavez, M., Hwang, D.U., 2006. Complex networks: structure and dynamics. *Phys. Rep.* 424, 175–308.
- Bogoni, J.A., Pires, J.S.R., Graipel, M.E., Peroni, N., Peres, C.A., 2018. Wish you were here: how defaunated is the Atlantic Forest biome of its medium- to large bodied mammal fauna? *PLoS ONE* 13(9), e0204515. <https://doi.org/10.1371/journal.pone.0204515>.
- Bogoni, J.A., da Silva, P.G., Peres, C.A., 2019. Co-declining mammal–dung beetle faunas

- throughout the Atlantic Forest biome of South America. *Echography* 42, 1803–1818.
- Busatta, S., 2007. The jaguar: the Aztecs' dark side of power. *Antrocom* 3 (1), 5–7.
- Callier, V., 2019. Solving Peto's Paradox to better understand cancer. *Proc. Nat. Acad. Sci.* 116 (6), 1825–1828.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241. <https://doi.org/10.1126/science.1116030>.
- Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J., Purvis, A., 2008. The predictability of extinction – biological and external correlates of decline in mammals. *Proc. R. Soc. B* 275, 1441–1448.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., 2012. Biodiversity loss and its impact on humanity. *Nature* 486, 59–67.
- Carvalho, C.S., Galetti, M., Colevatti, R.G., Jordano, P., 2016. Defaunation leads to microevolutionary changes in a tropical palm. *Sci. Rep.* 6, 31957. <https://doi.org/10.1038/srep31957>.
- Cassini, M.H., 1999. The evolution of reproductive systems in pinnipeds. *Behav. Ecol.* 10 (5), 612–616.
- Ceballos, G., Ehrlich, P.R., 2006. Global mammal distributions, biodiversity hotspots, and conservation. *Proc. Nat. Acad. Sci.* 103 (51), 19374–19379.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., Garcia, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* 2015 (1), e1400253. <https://doi.org/10.1126/sciadv.1400253>.
- Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Nat. Acad. Sci.* 114 (30), 6089–6096. <https://doi.org/10.1073/pnas.1704949114>.
- Chapin, F.S., Zavaletta, E.S., Eviner, V.T., Naylor, R.L., et al., 2000. Consequences of changing biodiversity. *Nature* 405, 234–242.
- Cormier, L., 2006. A preliminary review of neotropical primates in the subsistence and symbolism of indigenous lowland south American peoples. *Ecol. Environ. Anthropol.* 2 (1), 14–32.
- Cressie, N.A.C., 1993. *Statistics for Spatial Data*, Revised Edition. John Wiley & Sons Inc.
- Davidson, A.D., Hamilton, M.J., Boyer, A.G., Brown, J.H., Ceballos, G., 2009. Multiple ecological pathways to extinction in mammals. *Proc. Nat. Acad. Sci.* 106 (26), 10702–10705.
- Davidson, A.D., Detling, J.K., Brown, J.H., 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. *Front. Ecol. Environ.* 10 (9), 477–486. <https://doi.org/10.1890/110054>.
- Davis, M., Faurby, S., Svenning, J.-C., 2018. Mammal diversity will take millions of years to recover from the current biodiversity crisis. *Proc. Nat. Acad. Sci.* 115 (44), 11262–11267. <https://doi.org/10.1073/pnas.1804906115>.
- Debastiani, V.J., Pillar, V.D., 2012. SYNCOSA – R tool for analysis of metacommunities based on functional traits and phylogeny of the community components. *Bioinformatics* 28, 2067–2068.
- Dean, W., 1996. *With Broadax and Firebrand: The Destruction of the Brazilian Atlantic Forest*. University of California Press, California.
- Díaz, S., Purvis, A., Cornellissen, J.H.C., Mace, G.M., et al., 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecol. Evol.* 3 (9), 2958–2975.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. *Science* 345, 401–406.
- Dormann, C.F., Gruber, B., Freund, J., 2008. Introducing the bipartite package: analysing ecological networks. *R News* 8 (2), 8–11.
- Duffy, J.E., Godwin, C.M., Cardinale, B.J., 2017. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* 549, 261–264. <https://doi.org/10.1038/nature23886>.
- Espinosa, S., Branch, L.C., Cueva, R., 2014. Road development and the geography of hunting by an amazonian indigenous group: consequences for wildlife conservation. *PLoS ONE* 9 (12), e114916. <https://doi.org/10.1371/journal.pone.0114916>.
- Faurby, S., Davis, M., Pedersen, R.O., Schowaneck, S.D., Antonelli, A., Svenning, J.-C., 2018. *PHYLACINE 1.2: the phylogenetic atlas of mammal macroecology*. *Ecology* 99 (11), 2626–2626.
- Flynn, D.F.B., Mirotnichnick, N., Jain, M., Palmer, M.I., Naeem, S., 2011. Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. *Ecology* 92 (8), 1573–1581.
- Feeley, K.J., Stroud, J.T., 2018. Where on Earth are the “tropics”? *Front. Biogeogr.* 10 (2), e38649. <https://doi.org/10.21425/F5101-238649>.
- Galetti, M., Bovendorp, R.S., Guevara, R., 2015. Defaunation of large mammals leads to an increase in seed predation in the Atlantic forests. *Global Ecol. Conserv.* 3 (2015), 824–830.
- González-Maya, J.F., Martínez-Meyer, E., Medellín, R., Ceballos, G., 2017. Distribution of mammal functional diversity in the Neotropical realm: Influence of land-use and extinction risk. *PLoS ONE* 12 (4), e0175931.
- Gotelli, N.J., Graves, G.R., 1996. *Null Models in Ecology*. Smithsonian Institution Press.
- Guterres, A., Lemos, E.R.S., 2018. Hantaviruses and a neglected environmental determinant. *One Health* 5, 27–33.
- Harrison, P.A., Berry, P.M., Simpson, G., Haslett, J.R., et al., 2014. Linkages between biodiversity attributes and ecosystem services: a systematic review. *Ecosys. Serv.* 9, 191–203.
- Hausmann, N.S., 2017. Soil movement by burrowing mammals: a review comparing excavation size and rate to body mass of excavators. *Prog. Phys. Geogr.* 41 (1), 29–45.
- Hautier, Y., Saner, P., Philipson, C., Bagchi, R., Ong, R.C., et al., 2010. Effects of seed predators of different body size on seed mortality in bornean logged forest. *PLoS ONE* 5 (7), e11651. <https://doi.org/10.1371/journal.pone.0011651>.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75 (1), 3–35.
- Howe, H.E., Smallwood, J., 1982. Ecology of seed dispersal. *Annu. Rev. Ecol. Syst.* 13, 201–228.
- Hortal, J., Bello, F., Diniz-Filho, J.A.F., Lewinsohn, T.M., Lobo, J.M., Ladle, R.J., 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Ann. Rev. Ecol. Evol. System.* 46, 523–549.
- IUCN, 2018. *Spatial data download: Mammals*. Available at: <http://www.iucnredlist.org/technicaldocuments/spatial-data#mammals> (accessed: June-11-2018).
- Janzen, D.H., 1971. Seed Predation by Animals. *Annu. Rev. Ecol. Evol. Syst.* 2 (1), 465–492.
- Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., et al., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* 90 (9), 2648.
- Koch, A., Brierley, C., Maslin, M.M., Lewis, S.L., 2019. Earth system impacts of the European arrival and Great Dying in the Americas after 1492. *Quarter. Sci. Rev.* 207, 13–36.
- Kremen, C., 2005. Managing ecosystem services: what do we need to know about their ecology? *Ecol. Lett.* 2005 (8), 468–479.
- Kunz, T.H., Torrez, E.B., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. *Ann. N.Y. Acad. Sci.* 1223, 1–38.
- Kurten, E.L., 2013. Cascading effects of contemporaneous defaunation on tropical forests communities. *Biol. Conserv.* 163, 22–32.
- Lacher, T.E., Davidson, A.D., Fleming, T.H., Gómez-Ruiz, E.P., et al., 2019. The functional roles of mammals in ecosystems. *J. Mamm.* 100 (3), 942–964.
- Legendre, P., Fortin, M.J., Borcard, D., 2015. Should the Mantel test be used in spatial analysis? *Meth. Ecol. Evol.* 6, 1239–1247.
- Levi, T., Kilpatrick, A.M., Mangel, M., Wilmers, C.C., 2012. Deer, predators, and the emergence of Lyme disease. *Proc. Nat. Acad. Sci.* 109 (27), 10942–10947. <https://doi.org/10.1073/pnas.1204536109>.
- Machicote, M., Branch, L.C., Villareal, D., 2004. Burrowing owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? *Oikos* 106, 527–535.
- Májeková, M., Paal, T., Plowman, N.S., Bryndová, M., et al., 2016. Evaluating functional diversity: missing trait data and the importance of species abundance structure and data transformation. *PLoS ONE* 11 (2), e0149270. <https://doi.org/10.1371/journal.pone.0149270>.
- McConkey, K.R., O'Farrill, G., 2016. Loss of seed dispersal before the loss of seed dispersers. *Biol. Conserv.* 201, 38–49.
- MEA (Millennium Ecosystem Assessment), 2003. *Ecosystems and human well-being: a framework for assessment*. Island Press, Washington, D.C.
- MEA (Millennium Ecosystem Assessment), 2005. *Ecosystems and human well-being: biodiversity synthesis*. World Resources Institute, Washington, D.C.
- Meredith, R.W., Janecka, J.E., Gatesy, J., Ryder, O.A., et al., 2011. Impacts of the cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* 334, 521–524.
- Morrone, J.J., 2014. Biogeographical regionalisation of the Neotropical region. *Zootaxa* 3782 (1), 1–110.
- Naeem, S., 1998. Species redundancy and ecosystem reliability. *Conserv. Biol.* 12 (1), 39–45.
- Norconk, M.A., Grafton, B.W., Conklin-Britain, N.L., 1998. Seed dispersal by neotropical seed predators. *Am. J. Primat.* 45, 103–126.
- Ojeda, R.A., 2013. Diversity and conservation of Neotropical Mammals. *Encyclopedia of Biodiversity*, second ed. Academic Press, Waltham.
- Oliveira, B.F., Machac, A., Costa, G.C., Brooks, T.M., Davidson, A.D., Rondinini, C., Graham, C.H., 2016. Species and functional diversity accumulate differently in mammals. *Glob. Ecol. Biogeogr.* 25 (9), 1119–1130. <https://doi.org/10.1111/geb.12471>.
- Oliveira, U., Soares-Filho, B.S., Paglia, A.P., Brescovit, A.D., et al., 2017. Biodiversity conservation gaps in the Brazilian protected areas. *Sci. Rep.* 7, 9141. <https://doi.org/10.1038/s41598-017-08707-2>.
- Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., et al., 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51 (11), 933–938.
- Pacifici, M., Visconti, P., Butchart, S.H.M., Watson, J.E.M., Cassola, F.M., Rondinini, C., 2017. Species' traits influenced their response to recent climate change. *Nature Clim. Chan.* 7, 205–209.
- Pearson, K., 1900. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. *Phil. Mag. Series* 50 (302), 157–175.
- Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. *Comp. Geosci.* 30, 683–691.
- Peres, C.A., 1990. Effects of hunting on western amazonian primate communities. *Biol. Conserv.* 54, 47–59.
- Peres, C.A., Dolman, P., 2000. Density compensation in neotropical primate communities: evidence from 56 hunted and non-hunted Amazonian forests of varying productivity. *Oecologia* 122, 175–189.
- Peres, C.A., 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conserv. Biol.* 15 (6), 1490–1505.
- Peres, C.A., Emilio, T., Schiatti, J., Desmoulière, S.J.M., Levi, T., 2016. Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Nat. Acad. Sci.* 113 (4), 892–897.
- Peres, C.A., Schiesari, L.G., Dias-Leme, C.L., 1997. Vertebrate predation of Brazil-nuts (*Bertholletia excelsa*, Lecynthidaceae), an agouti-dispersed Amazonian seed crop: a test of the escape hypothesis. *J. Trop. Ecol.* 13, 69–79.
- Peters, R.H., 1983. *The Ecological Implications of Body Size*. Cambridge University Press, New York.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberst, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of

- extinction, distribution, and protection. *Science* 344 (6187), 987–999.
- Pretty, J., Adams, B., Berkes, F., Athayde, S.F., et al., 2009. The Intersections of Biological Diversity and Cultural Diversity: Towards Integration. *Conserv. Soc.* 7 (2), 100–112.
- R. Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.
- Redford, K.H., 1992. The empty forest. *Bioscience* 42, 412–422.
- Redford, K.H., Robinson, J.G., 1987. The game of choice: Patterns of Indian and Colonist hunting in the Neotropics. *Am. Anthropol.* 89, 650–667.
- Reichman, O.J., Smith, S.C., 1990. Burrows and Burrowing Behaviour by Mammals. In: Genowais, H.H. (Ed.), *Current Mammalogy*. Plenum Press, New York, pp. 197–244.
- Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E.L., Pavoine, S., 2016. Measuring the functional redundancy of biological communities: a quantitative guide. *Meth. Ecol. Evol.* 7, 1386–1395.
- Ripple, W.J., Abernethy, K., Betts, M.G., Chapron, G., et al., 2016. Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science* 3, 160498.
- Rodrigues, T.F., Mantellatto, A.M.B., Superina, M., Chiarello, A.G., 2019. Ecosystem services provided by armadillos. *Biol. Rev.* <https://doi.org/10.1111/brv.12551>.
- Roemer, G.W., Gompper, M.E., Van Valkenburgh, B., 2009. The Ecological Role of the Mammalian Mesocarnivore. *BioScience* 59, 165–173.
- Rondinini, C., Di Marco, M., Chiozza, F., Santulli, G., et al., 2011. Global habitat suitability models of terrestrial mammals. *Phil. Trans. R. Soc. B.* 366, 2633–2641.
- Ross, E., 1978. Food Taboos, Diet, and Hunting Strategy: The Adaptation to Animals in Amazon Cultural Ecology. *Current Anthropol.* 19, 1–19.
- Safi, K., Cianciaruso, M.V., Loyola, R., Brito, D., Armour-Marshall, K., Diniz-Filho, J.A.F., 2011. Understanding global patterns of mammalian functional and phylogenetic diversity. *Phil. Trans. R. Soc. B.* 366, 2536–2544. <https://doi.org/10.1098/rstb.2011.0024>.
- Schweiger, A.K., Cavender-Bares, J., Townsend, P.A., Hobbie, S.E., et al., 2018. Plant spectral diversity integrates functional and phylogenetic components of biodiversity and predicts ecosystem function. *Nature Ecol. Evol.* 2, 976–982.
- Salvador, S., Clavero, M., Pitman, R.L., 2011. Large mammal species richness and habitat use in an upper Amazonian forest used for ecotourism. *Mamm. Biol.* 76, 115–123.
- Schultz, J., 2005. *The Ecozones of the World: The Ecological Divisions of the Geosphere*. Springer, Berlin.
- Seidensticker, J., 2016. Biodiversity resilience in the Central Indian Highlands is contingent on maintaining and recovering landscape connectivity: the tiger as a case study. *Reg. Environ. Change* 16 (1), 167–179.
- Shiels, A.B., González, G., Lodge, D.J., Willing, M.R., Zimmerman, J.K., 2015. Cascading Effects of Canopy Opening and Debris Deposition from a Large-Scale Hurricane Experiment in a Tropical Rain Forest. *BioScience* 65, 871–881.
- Stafford, C.A., Preziosi, R.F., Sellers, W.I., 2017. A pan-neotropical analysis of hunting preferences. *Biodivers. Conserv.* 26, 1877–1897. <https://doi.org/10.1007/s10531-017-1334-8>.
- Strona, G., Bradshaw, C.J.A., 2018. Co-extinctions annihilate planetary life during extreme environmental change. *Sci. Rep.* 8, 16724. <https://doi.org/10.1038/s41598-018-35068-1>.
- Surovell, T.A., Pelton, S.R., Anderson-Sprecher, R., Myers, A.D., 2016. Test of Martin's overkill hypothesis using radiocarbon dates on extinct megafauna. *Proc. Nat. Acad. Sci.* 113 (4), 886–891.
- Terborgh, J., 1988. The big things that run the World: a sequel to E. O. Wilson. *Conserv. Biol.* 2 (4), 402–403.
- Tilman, D., 1996. Biodiversity: population versus ecosystem stability. *Ecology* 77 (2), 350–363.
- Tilman, D., 2001. Functional diversity. *Encyc. Biodiv.* 3, 109–121.
- Tortato, F.R., Izzo, T.J., Hoogesteijn, R., Peres, C.A., 2017. The numbers of the beast: valuation of jaguar (*Panthera onca*) tourism and cattle depredation in the Brazilian Pantanal. *Glob. Ecol. Conserv.* 11, 106–114.
- Trites, A.W., 2002. Predator-prey relationships. In: Perrin, W.F., Wursig, B., Thewissen, H.G.M. (Eds.), *Encyclopedia of Marine Mammals*. Academic Press, San Diego, pp. 994–997.
- Udvardy, M.D.F., 1975. A Classification of the Biogeographical Provinces of the World. IUCN Occasional Papers n° 18.
- Ulbrich, K., Settele, J., Benedict, F.F., 2010. In: Ulbrich, K., Settele, J., Benedict, F.F. (Eds.), *Biodiversity in Education for Sustainable Development – Reflection on School-Research Cooperation*. Pensoft Publishers, Sofia–Moscow.
- Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89, 2290–2301.
- Wallach, A.D., Izhaki, I., Toms, J.D., Ripple, W.J., Shanas, U., 2015. What is an apex predator? *Oikos* 124, 1453–1461.
- Wenny, D.G., 2000. Seed Dispersal, Seed Predation, and Seedling Recruitment of a Neotropical Montane Tree. *Ecol. Monogr.* 70 (2), 331–351.
- Wilman, H., Belmaker, J., Simpson, J., Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. Elton Traits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* 95 (7) 2027–2027.
- Zhou, Y., Buesching, C.D., Newman, C., Kaneko, Y., Xie, Z., MacDonald, D.W., 2013. Balancing the benefits of ecotourism and development: The effects of visitor trail-use on mammals in a Protected Area in rapidly developing China. *Biol. Conserv.* 165, 18–24.