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REVIEW

Productivity correlates positively with mammalian diversity independently of the species' feeding guild, body mass, or the vertical strata explored by the species

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ABSTRACT

1. Mammals can influence ecosystem functioning through essential ecological processes. In patchy landscapes, mammalian diversity can be correlated with ecosystem productivity through its effect on resource availability. However, mammals comprise species with contrasting habitat use and requirements, and it is unknown whether the diversity–productivity relationship changes as a function of the mammal species' traits.
2. We use meta-analytical techniques to quantify the effect and assess whether mammal species richness and abundance correlates positively with productivity. Further, we assess whether the diversity–productivity relationship is influenced by the species' body mass (<1 kg: small, and >1 kg: large, and mixed small and large), the vertical strata explored by the species (terrestrial, arboreal, and mixed terrestrial and arboreal species), and the species' feeding guild (herbivore, omnivore, insectivore, and mixed feeding guilds).
3. In total, 53 studies fitted the eligibility criteria worldwide, comprising 285 different effect sizes representing the magnitude of the mammal diversity–productivity relationship in six biogeographical realms. Ecosystem productivity was quantified with various surrogate variables, such as soil nutrients, annual rainfall, above-ground production, evapotranspiration, net primary production, plant cover, and elevation.
4. The relationships between productivity measures and both mammal species richness and abundance were significant and positive. Mammal diversity

correlated positively with ecosystem productivity, for mammal species differing in body mass, the vertical strata explored by species (except arboreal mammals), and feeding guilds (except insectivorous mammals). Overall, this result supports the view that diversity in the entire mammal community is positively related to increasing productivity.

5. Sites with greater ecosystem productivity are usually associated with more resources and higher ecosystem carrying capacity, which provide greater resilience to human disturbance than less productive sites. Thus, quantifying productivity can help researchers to identify critical areas for restoration and to propose effective guidelines for mammal conservation.

INTRODUCTION

Ecosystem productivity has a pervasive relationship with species diversity (Waide et al. 1999, Mittelbach et al. 2001, Reed et al. 2006). Productivity can be defined as the rate of energy flow to an ecological system (Abrams 1995, Rosenzweig 1995, Waide et al. 1999, Gaston 2000, Mittelbach et al. 2001). Researchers have found different relationships: there are positive (Kaufman & Willig 1998, Ferreira Neto et al. 2021b), negative (Peres 1997, Zhang & Ouyang 2019), unimodal (Ganzhorn et al. 1997, Gebert et al. 2019), U-shaped (Shepherd 1998, Chen et al. 2020), and even non-significant relationships between productivity and diversity (Williams & Marsh 1998, Ramírez-Bautista & Williams 2019). Depending on the underlying mechanism, hypotheses relating to productivity may also be mediated by the spatial extent investigated, which may also explain variation in diversity patterns (Currie 1991, Chase & Leibold 2002, Hawkins et al. 2003, Gonzalez-Megias et al. 2007, Veech & Crist 2007, Hortal et al. 2008, Swan et al. 2020). This idiosyncrasy in the diversity–productivity relationship has been observed in various taxonomic groups, such as birds (Aves), reptiles (Reptilia), and termites (Isoptera; Mittelbach et al. 2001), and remains contentious for mammals (Fritz et al. 2016).

Several hypotheses may explain variation in mammal species richness and abundance in relation to productivity or energy (Hutchinson 1959, Wright 1983), environmental stability (Fjeldsaå & Lovett 1997), and habitat heterogeneity (Hamilton et al. 2020). The species–energy hypothesis predicts that variations in species richness and distribution are related to physical environment and productivity per unit area (Wright 1983). Another hypothesis proposes that energy available in the environment affects the number of individuals and therefore the number of species in communities, hence driving the accumulation of species over space and time (Allen et al. 2007, Hurlbert & Stegen 2014). Productivity can be a determinant driver for the physiological requirements of organisms ('ambient energy hypothesis'; Turner et al. 1987). Also, animal diversity is limited by the production of food sources, such as plant biomass for herbivores ('productivity hypothesis'; Huston 2014). This resource limitation would affect animal size so that larger animals should inhabit more productive areas because of their higher energetic requirements for metabolic demands (McNab 1963).

Productivity can be correlated with soil quality, as plants growing in richer soils may invest more energy in reproduction than in secondary compound or root production (Quesada et al. 2010, 2012), which results in a greater investment in fruit yields (Chave et al. 2010). Lower investment in secondary compounds makes the leaves more easily digestible for fauna of various body sizes (Coley et al. 1985), leading to increased herbivory (Pilbeam 2018). These mechanisms may scale up through the trophic web, increasing energy availability and affecting the number of individuals and species richness of arboreal (Peres 2008) or terrestrial mammals (Ferreira Neto et al. 2021a). While some of these productivity proxies are direct measures of plant biomass or cover, which could influence mammal diversity due to an influence on resource availability, some of them are coarse proxies, which could influence mammal diversity indirectly (Mittelbach et al. 2001, Groner & Novoplansky 2003, Hillebrand & Cardinale 2010). For instance, researchers measuring productivity with elevation or rainfall descriptors often assume that these measures are correlated with plant diversity, cover, or biomass and that this productivity effect would drive mammal diversity (Letnic et al. 2011, Ramírez-Bautista & Williams 2019).

Ecosystem productivity tends to be higher in more complex and heterogeneous environments (Hamilton et al. 2020), and high productivity offers more resources, which favour the establishment of species with various traits (e.g. feeding guilds, vertical strata explored by species, and body sizes; Oliveira et al. 2016). Therefore, ecosystem productivity may be more closely linked to some particular traits than to others. Larger herbivorous mammals need greater plant abundance to sustain themselves, whereas smaller herbivorous mammals may persist with a lower abundance of plants, especially if these plants are of superior quality (Olff et al. 2002). For instance, larger

mammals are expected to occur in more productive sites (McNab 1963, Daskin & Pringle 2016). Besides body size, the relationship between productivity and mammal diversity may change due to the vertical strata explored by the species. The diversity of arboreal mammals, for instance, may be closely related to productivity, because arboreal mammals feed on large quantities of seeds, fruits, and flowers (Wormington et al. 2007). They may have priority access to food sources produced in the canopy, before they fall and become available for the terrestrial fauna (Peres 2008). Productivity may have also different impacts on species of different feeding guilds. Forest productivity is more closely related to herbivorous rodent diversity than to the diversity of predatory insectivorous small mammals (shrews; Niedziałkowska et al. 2010).

Researchers have corroborated the relationship between productivity and both species richness and individual abundance of mammals on several continents. Some remarkable examples are marsupials in Australia (Pavey et al. 2014, Swan et al. 2020), arboreal mammals in Asia (Wang et al. 2013), ungulates in Africa (Kimuyu et al. 2017), and terrestrial mammals in South America (Ferreira Neto et al. 2021a). However, whether or how much mammalian body mass, feeding guilds, and vertical strata explored by the species influence the diversity–productivity relationship is not fully understood (Brown 1981, 2014). We compared patterns of terrestrial and arboreal mammalian diversity with ecosystem productivity measures at various spatial extents and in six biogeographical realms. Our objectives were as follows: 1) to quantify the relationship between productivity and mammal diversity worldwide; and 2) to assess how much of the relationship between productivity and mammal diversity metrics (abundance and species richness) can be explained by mammal body mass, vertical strata explored by the species, and feeding guilds. Specifically, we predicted that herbivorous species, larger mammals, and arboreal mammals would present a stronger relationship between productivity and diversity than predatory species, smaller mammals, and terrestrial mammals. This expectation is justified because large mammal species require more energy to sustain their metabolism than small ones (Olff et al. 2002). Furthermore, arboreal and herbivorous mammals are directly linked to plant species to sustain their growth, due to their habitat exploration or feeding (Kuijper & Bakker 2005, Wormington et al. 2007, Peres 2008), and thus, we expected a closer relationship of these groups with productivity in comparison with species exploring other vertical strata and in other feeding guilds.

METHODS

Search and study selection

This work was carried out in accordance with the recommendations of the PRISMA initiative (Preferred Reporting Items for Systematic Reviews and Meta-Analyses; Moher et al. 2009). The search for the studies was conducted on 20 May 2019, in the ISI Web of Science database (currently managed by Clarivate Analytics); it included all publications until the year 2019. The combination of the following keywords and Boolean arguments was used to search the ISI: ("primary productivity" OR "productivity" OR "resource availability" OR "resource diversity" OR "soil fertility" OR "rainfall" OR "NPP" OR "net productivity") AND ("mammal*" OR "vertebrate*"). This set of keywords and Boolean arguments was applied to the 'topic' search without filters.

The abstracts of all 4312 studies returned by the keyword search were evaluated, and we excluded those studies that were out of scope of this meta-analysis (they did not evaluate the diversity–productivity relationship; 4250 studies) or that had no relevant information for our synthesis, such as sample size, mean, or standard deviation (nine studies; Appendix S1). We included in our meta-analysis only 53 studies that tested the mammalian diversity–productivity relationship and for which standard measures of effect sizes (differences between means or correlations) could be estimated. Studies were also excluded if their level for analysis had a sample size of < 4 (e.g. carnivorous feeding guild, volant vertical strata, and biomass species diversity metric). We focused on non-flying mammals, given that bats present a high ability to disperse compared with arboreal and terrestrial forest mammals.

To evaluate the consistency of the screening method, two authors independently screened the abstracts of a random sample of 25% of the studies returned by the Web of Science search. The concordance between both screenings was assessed using the kappa statistic (κ; Côté et al. 2013). Considering values of kappa equal to 0.6 as substantial (following Côté et al. 2013), we found a sufficient concordance between the different authors about which papers should be included in the meta-analysis ($\kappa = 0.68$).

Data extraction

All 53 studies retained for synthesis assessed the relationship between proxies of ecosystem productivity and mammal assemblages, using correlative experimental designs. Several studies reported more than one correlation so that the sample size (number of effect sizes) was 285. For each correlation, we recorded the sample sizes and correlation coefficients (Pearson's r or Spearman's ρ), or coefficient of determination (r^2) from a simple regression between productivity and diversity of mammals. In six studies that did not provide any type of correlation, r^2, mean, or standard deviation to calculate the effect size, but did provide a graph, we used the *metaDigitise* package (Pick et al. 2018) to estimate r values.

We also recorded a set of variables describing the group of mammals assessed and other study characteristics that could be used as moderator variables. We observed whether the authors measured productivity via soil nutrients (four studies, e.g. Rodríguez & Ojeda 2015), annual rainfall (23 studies, e.g. Martín-Regalado et al. 2019), above-ground production (four studies, e.g. Niedziałkowska et al. 2010), evapotranspiration (eight studies, e.g. Jiménez-Alfaro et al. 2016), normalised difference vegetation index (five studies, e.g. Qian 2010), net primary production (10 studies, e.g. Zhang & Ouyang 2019), plant cover (five studies, e.g. Kimuyu et al. 2017), elevation (21 studies, e.g. Ramírez-Bautista & Williams 2019), or latitude (one study, Currie 1991). Some studies used more than one measure of productivity. The spatial extent covered by each study was quantified as the distance (in km) between the farthest apart study sites, measured from the maps provided or derived from the text.

Diversity metrics were categorised as abundance and species richness. Other types of species diversity (e.g. Shannon index, Simpson index) and biomass did not fit the eligibility criteria for the analysis (number of studies < 4) and were therefore excluded. We considered as abundance the total number of individuals collected (Stanley et al. 2014), density (Kimuyu et al. 2017), total number of captures (Torre & Arrizabalaga 2009), annual capture rates (Dickman et al. 1999), mean density of rodents (Jędrzejewski & Jędrzejewska 1996), or summer density (Shenbrot et al. 2010). We considered species richness as the total number of species recorded in a given community (e.g. McCain et al. 2018).

We obtained information on feeding guilds, mammalian orders, common names, vertical strata explored by species, and body mass from the literature (Wilson & Reeder 2005, Nowak 2018). Mammals included in each correlation were classified based on their characteristics of traits as follows: vertical strata explored by species (terrestrial, arboreal, and mixed strata), feeding guilds (herbivores, insectivores, omnivores, and mixed feeding guilds), and body mass (small, large, and mixed mass; Table 1). Arboreal mammals were defined as those specialised in climbing trees by the use of gripping feet (Andrews & O'Brien 2000). We considered mammals weighing less than 1 kg as small mammals and those weighing more than 1 kg as large (Peres 2000). We used the term 'mixed' to describe all studies that included two or more groups of mammals with different vertical strata explored by species, different body masses, or different feeding guilds (e.g. herbivores and omnivores in the same study). Neither volant mammals nor carnivorous mammals fitted the eligibility criteria to be included in the study (we found < 4 studies for each). Scansorial mammals were grouped together with arboreal mammals because of their low number of studies and similar habitat use. We also identified the biogeographical realm in which each study took place (Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, and Palearctic regions; Fig. 1).

Data analysis

We transformed all correlation coefficients to the Pearson product–moment correlation coefficient (r). Thirteen studies comprised 35 effect sizes presenting as the Spearman correlation coefficient (ρ), which was transformed by the following equation (Lajeunesse et al. 2013): $r = 2^{*}\sin(\pi\rho/6)$, if $n < 90$; or $r = \rho$, if $n \geq 90$, where n represents the sample size. All 53 studies presented coefficients of determination (r^2) of a simple regression between productivity and mammal diversity. In these cases, we estimated r as the square root of r^2. Next, we transformed all r values to Fisher's z (and their respective variances), following Borenstein et al. (2009).

We estimated a weighted effect size using a random-effects model. In a random-effects model, we assume that all studies do not share a common true effect size, but they do share a mean true effect size with a given true

Table 1. Categories of body mass, vertical strata explored by species, and feeding guilds of mammals that were adopted to classify the studies. Mixed: studies that estimated mammal diversity without separating species by functional trait

Moderator	Categories	Details
Body mass	Large	Mammals weighing more than 1 kg
	Mixed	Large and small mammals were considered together
	Small	Mammals weighing less than 1 kg
Vertical strata explored by species	Arboreal	Species specialised in climbing trees, including scansorial species.
	Mixed	Mammals exploring various vertical strata were considered together
	Terrestrial	Species adapted to live predominantly or entirely on land
Feeding guilds	Herbivore	Feeding on plant material
	Insectivore	Subsisting primarily on insects and other invertebrates
	Omnivore	Species adapted to feed on plant and animal matter
	Mixed	Mammals with different feeding groups were considered together

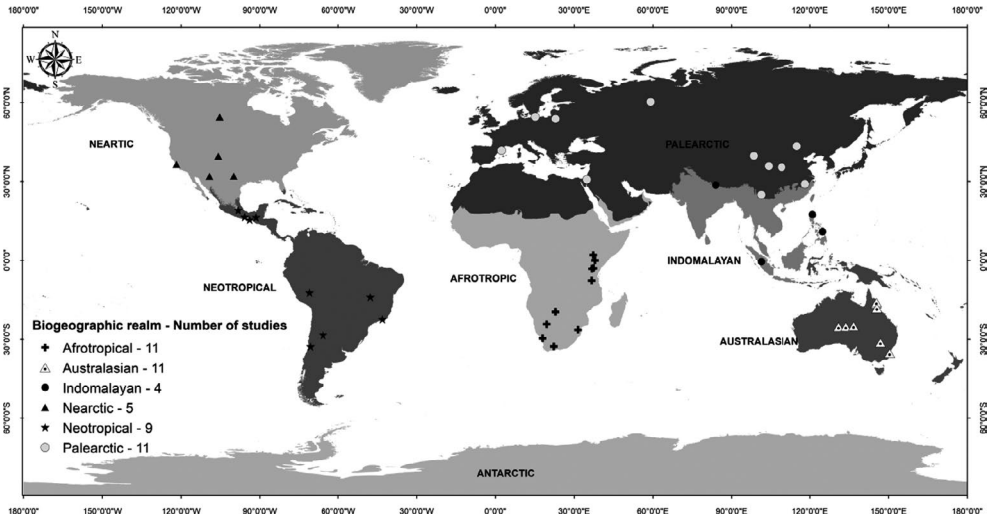

Fig. 1. Map of the studies included per biogeographical realm.

variance between studies (T^2; Borenstein et al. 2009, 2017). We estimated T^2 by restricted maximum-likelihood and weighted each effect size by the inverse of total variance (effect-size variance plus T^2). We quantified the heterogeneity in study outcomes (effect sizes summarising mammal diversity–productivity) with the T^2_{Between} and I^2 statistics (Borenstein et al. 2009, 2017). The T^2_{Between} statistic is the between-study variance, a heterogeneity measure in the scale of effect-sizes (Borenstein et al. 2009, 2017). The I^2 statistic measures how much of the heterogeneity is true variability (i.e. not due to experimental error); it is measured on a relative scale (Borenstein et al. 2009, 2017). We also reported Cochrane's Q, which is the weighted sum of squared differences between individual study effects and the pooled effect across studies (Koricheva et al. 2013).

We assessed the effects of vertical strata explored by species (levels: arboreal, terrestrial, and mixed), feeding guilds (levels: herbivore, insectivore, mixed, and omnivore), and body size (levels: small, large, and mixed) on Fisher's z to quantify how much of the heterogeneity (variability in study outcomes) could be explained by these characteristics. The effects of these categorical moderators ('explanatory variables' in meta-analyses) on the relationship between mammal diversity and productivity (Fisher's z; response variable) were evaluated by subgroup analyses (Borenstein et al. 2009, 2017), which were performed separately for each moderator. The effect of each moderator was assessed by partitioning Cochrane's Q into heterogeneity explained by the moderator variable (QM) and residual heterogeneity (analogous to an analysis of variance; Borenstein et al. 2009). The QM follows a χ^2 distribution and, if significant, indicates a difference between the mean effect size of at least one of the levels of the moderator considered (in other words, the moderator explains part of the heterogeneity). We also tested the subgroup models without intercepts to determine whether the mean effect size of each moderator level differed from zero.

The effects of the spatial extent on the relationship between productivity and mammal diversity (Fisher's z) were evaluated by a meta-regression (Borenstein et al. 2009). In the meta-regression, the effect size (Fisher's z) was the response variable and the study's spatial extent was the moderator variable. The spatial extent was log-transformed to ameliorate linearity.

In several cases, we estimated several effect sizes measured for a single study. For example, Martín-Regalado et al. (2019) correlated different metrics of productivity such as net primary production, rainfall, evapotranspiration, and elevation with species richness and abundance of rodents in southern Mexico. However, in this case, effect sizes cannot be assumed to be independent because they were estimated with the same sampling units (a multiplicity artefact; Hedges et al. 2010, López-López et al. 2018). Thus, to control for effect-size multiplicity, the cumulative effect size and subgroup analyses consisted of multi-level meta-analyses (Nakagawa & Santos 2012). In the multi-level meta-analysis, we controlled for multiplicity by adding a random-effects term encoding the study and corresponding to the group of dependent effect sizes ($T^2_{\text{study-level}}$; Nakagawa & Santos 2012).

We used a cumulative meta-analysis to explore how the relationship between productivity and mammal diversity varied over time. Evidence is not static and tends to change over time as a function of changes in research methods or characteristics of the subjects (Koricheva et al. 2013). For instance,

meta-analyses on different ecological subjects found that the mean effect describing a relationship decreases with time, such as the impact of introduced species on native species richness (Crystal-Ornelas & Lockwood 2020), or the effect of volatile plant communication on herbivory (Karban et al. 2014). In a cumulative meta-analysis, a series of sequential meta-analyses are conducted, with studies ordered chronologically (Leimu & Koricheva 2004, Borenstein et al. 2009). First, a weighted effect size is computed with the oldest study, and then, a second weighted effect size is computed with the two oldest studies and so on, until the final weighted effect size is computed with all studies included in the meta-analysis. To avoid the influence of multiplicity, we conducted the cumulative meta-analysis with mean effect sizes and variances by study.

To assess for publication bias, we used a funnel plot to identify asymmetry in the publications on productivity and mammal diversity. The funnel plot, a scatterplot of effect sizes against a measure of their precision, tends to be symmetric around the mean effect size in the absence of bias (Borenstein et al. 2009). We further used the trim-and-fill method to 1) estimate the potential number of missing studies; and 2) correct the cumulated effect size by accounting for the potential omission of studies due to publication bias (Jennions et al. 2013). Finally, we also used Orwin's fail–safe number (Orwin 1983) to assess for publication bias. Orwin's fail–safe number estimates how many studies would need to be included to reduce the (unweighted) mean effect size to a desired threshold deemed as non-relevant (Borenstein et al. 2009, 2017). We chose non-relevant reductions to 25% of the mean effect size. For publication bias analyses, we computed mean effect sizes and variances by study to avoid bias due to multiplicity. All analyses were performed using the *metafor* package (Viechtbauer 2010) in R software.

RESULTS

Eleven studies were conducted in each of the Afrotropical, Australasian, and Palearctic regions, nine studies in the Neotropical region, five studies in the Nearctic region, and four studies in the Indomalayan region (Fig. 1). The other two continental-scale studies are not shown in Fig. 1.

For the 285 effect sizes, Fisher's z ranged from -2.17 ($r \approx -0.97$) to 3.58 ($r \approx 0.998$), and the weighted mean effect size was equal to 0.40 (95% confidence intervals ± 0.17, $k = 53$, $z = 4.68$, $P < 0.001$; Fig. 2). The heterogeneity in the relationship between productivity and diversity (species richness and abundance) was statistically significant (Q = 5417.83, degrees of freedom, d.f. = 284, $P < 0.001$, $k = 53$). The between-studies heterogeneity (T^2_{Between}) in the diversity–productivity relationship was equal to 0.20, and the study-level heterogeneity ($T^2_{\text{Study-level}}$) was 0.29. Approximately 97% of the heterogeneity was due to true variance among studies ($I^2 = 0.97$); in other words, almost all the variation in outcomes can potentially be explained by moderator variables describing differences among studies.

The diversity–productivity relationship did not vary as a function of feeding guilds (QM = 0.93, d.f. = 3, $P = 0.819$), body mass (QM = 0.01, d.f. = 2, $P = 0.993$), vertical strata explored by species (QM = 1.75, d.f. = 2, $P = 0.416$), or how diversity was quantified (as species richness or abundance; QM = 0.21, d.f. = 1, $P = 0.644$). Also, the diversity–productivity relationship for insectivorous and arboreal species did not differ from zero; in other words, there was no significant relationship (Fig. 3). The spatial extent of 43 studies ranged from 1.5 to 9000 km (median = 90 km), and 75% of the studies had a spatial extent of up to 337.5 km. Effect sizes were not significantly correlated with the spatial extent (QM = 0.74, df = 1, $P = 0.391$, k = 43), meaning that variation in the spatial extent of studies did not affect the relationship between productivity and mammal diversity.

Cumulative meta-analysis and publication bias assessment

The cumulative meta-analysis indicated that the effect sizes changed from 1984 to 2019 (Fig. 4). The oldest study we included estimated a strong, positive, and significant relationship between productivity and mammal diversity (East 1984); thereafter, this effect was reduced and became non-significant when a weighted mean effect size was calculated with the two oldest studies. After the inclusion of the third-oldest study and more recent studies, the weighted mean effect size became consistently positive. From 1997 to 2011, there was a pronounced decay in the magnitude of the weighted mean effect size. From 2011 onwards, the weighted mean effect size did not change considerably.

A funnel plot (scatterplot of productivity and its standard error) did not indicate asymmetry (Fig. 5). The trim-and-fill procedure indicated that no study was omitted due to a potential publication bias; therefore, there was no change in the corrected estimate including omitted studies from which we observed. Orwin's fail–safe number indicated that it would be necessary to include 159 additional studies to reduce the mean effect size to a quarter of its observed value. In sum, these analyses indicated that our results are robust to a potential publication bias.

DISCUSSION

We found that the diversity–productivity relationship was positive for all mammal trait groups and spatial extents.

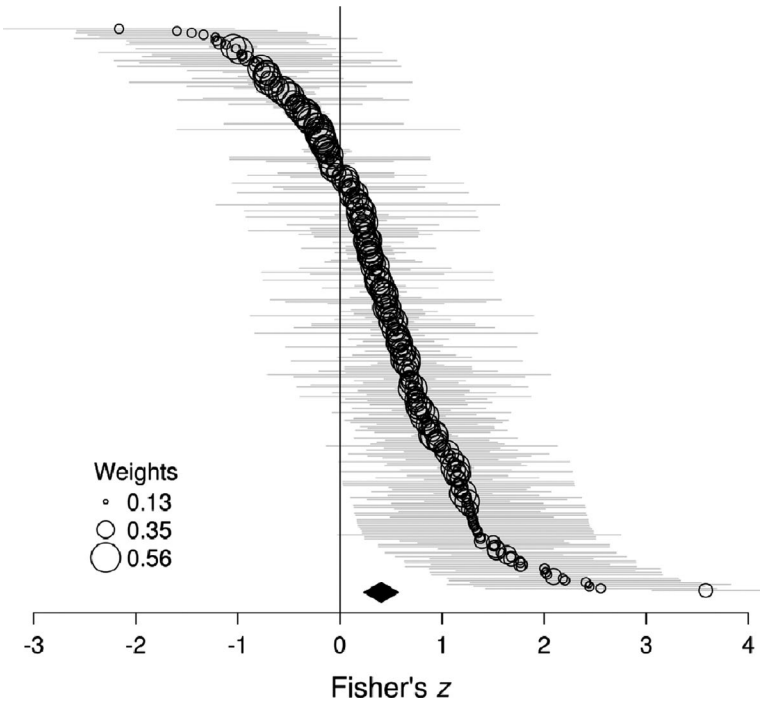

Fig. 2. Forest plot of the relationship between ecosystem productivity and mammal diversity in the 285 effect sizes taken from 53 studies. The effect sizes are ordered by increasing the magnitude of the mammal diversity–productivity relationship. Horizontal grey lines represent the 95% confidence intervals. The closed diamond represents the weighted mean effect size.

The diversity of large, small, and mixed-sized mammals was equally related to ecosystem productivity. Feeding guilds of mammals also tended to present a positive relationship between productivity and diversity, with the exception of insectivorous mammals. In addition, the diversity of terrestrial mammals, on average, was correlated with ecosystem productivity, whereas that of arboreal mammals was not (Fig. 3).

Consistency of diversity–productivity relationship across traits and scale

We hypothesised that herbivorous mammals would respond positively to increased productivity, because herbivores are more closely related to environmental primary productivity at the bottom of the food chain (Kuijper & Bakker 2005). For instance, more productive forests can offer more food sources, such as soft-tissue plants and seeds of trees, which support a more diverse array of herbivore species and more individuals (Jędrzejewski & Jędrzejewska 1996). We found that the diversity of omnivorous and mixed mammals was positively related to productivity, as was the diversity of herbivores (Fig. 3). This pattern is supported by a regional-scale study in north-eastern Poland, where the diversity of herbivorous, folivorous, and granivorous mammals was positively correlated with productivity; this was not the case for the diversity of insectivorous mammals (Niedziałkowska et al. 2010). Predatory species, such as insectivorous mammals, base their diet on food sources such as invertebrates and not directly on plant material, making them more resilient and able to exploit environments with different productivity levels (Niedziałkowska et al. 2010). The diversity–productivity relationship also differed between insectivorous small mammals and rodents and between large and small mammals along an elevational gradient in south-western China (Chen et al. 2017).

Productivity can have different effects on terrestrial and arboreal mammals. We hypothesised that productivity would be strongly correlated with the diversity of arboreal mammals because of strong bottom-up control of their abundance and diversity due to resource availability (Peres 2008). The bottom-up mechanism means that a lower trophic level, by limitation or quality of resources, affects the community structure of higher trophic levels (Power 1992), such as mammals (Lobo 2014). However, we found that the diversity of terrestrial mammals, on average, was positively correlated with productivity, whereas the diversity of arboreal mammals was not. One possible explanation is that arboreal mammals have direct access to fruits and leaves in the canopy (Wormington et al. 2007). The

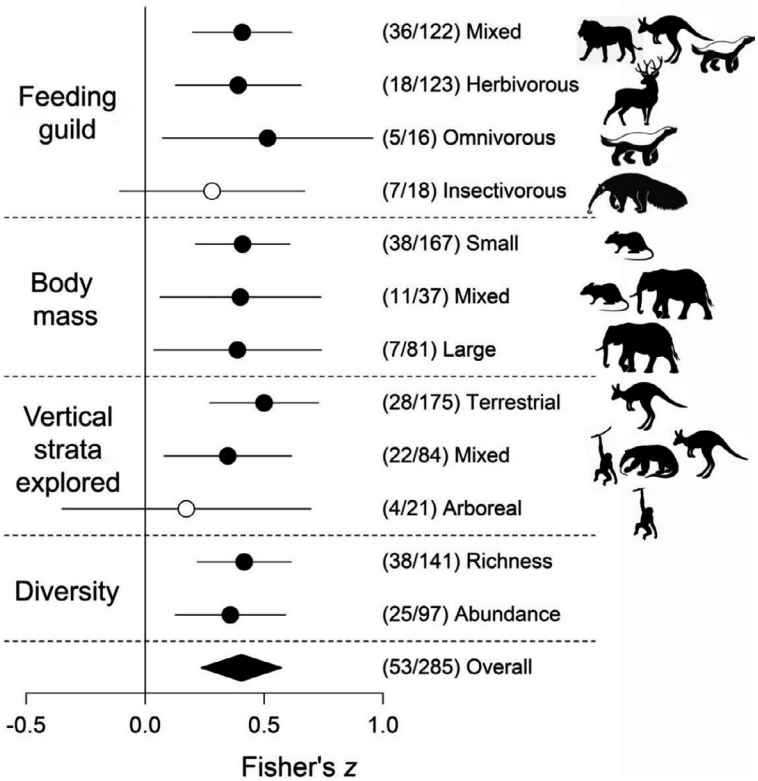

Fig. 3. Variation in the diversity–productivity relationship in mammals, in relation to feeding guilds, body mass, vertical strata explored by species and how diversity was quantified (as species richness or abundance). Circles and horizontal bars represent the mean effect sizes and the 95% confidence intervals, respectively. The vertical line indicates an effect size equal to zero. The closed diamond represents the weighted mean effect size. Numbers in parentheses represent the number of studies / the number of effect sizes. Open circles represent mean effect sizes that do not differ from zero. Closed symbols (circles and diamond) represent positive and significant mean effect sizes.

diversity–productivity relationship could also be affected by how species richness and abundance are quantified (Mittelbach et al. 2001). Another explanation is methodological, since diversity of terrestrial mammals is usually estimated by camera traps (O'Connell et al. 2010), whereas diversity of arboreal mammals is generally determined by applying linear transect methods (Peres 1999).

The diversity–productivity relationship tends to be unimodal at smaller scales where diversity peaks at intermediate productivity, but assumes a positive linear relationship when investigated at larger spatial scales (Chase & Leibold 2002). Most studies (75%) included in this review sampled over a spatial extent of up to 400 km, which may explain why the diversity–productivity relationship was unrelated to the spatial extent of the study. This result also suggests that the diversity–productivity relationship was more properly described at local than at regional scales. For instance, productivity is equivalent to climate variation in explaining the species richness of several animal groups, including mammals, at larger spatial scales (>800 km; Hawkins et al. 2003). Due to the variability in the design and analyses of the studies investigated here, the effect of the spatial extent on the diversity–productivity relationship in mammals requires further investigation.

Bias and knowledge shortfall in diversity–productivity relationship literature

Studies are more likely to be published when they detect a large and statistically significant effect (Møller & Jennions 2001, Borenstein et al. 2009). Over time, the accumulation of evidence from different systems tends to reduce the mean effect, as studies are published that do not support the hypothesis or show smaller effects (Leimu & Koricheva 2004, Crystal-Ornelas & Lockwood 2020). We observed a temporal reduction in the magnitude of the relationship between productivity and mammal diversity. The temporal reduction trend was most pronounced from 1997 to 2011 (Fig. 4). The inclusion of early studies that presented a weaker diversity–productivity relationship or even a negative correlation as opposed to the previous mean effect produces a steep decrease due to the

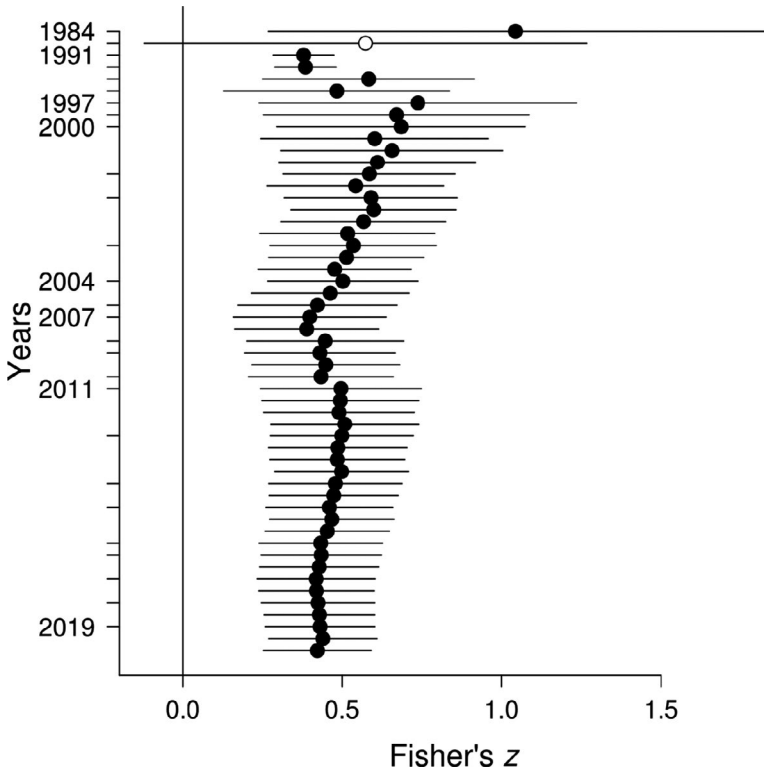

Fig. 4. Variation in the relationship between ecosystem productivity and mammal diversity (weighted mean effect size) over time (year of publication of the 53 studies included in the review is shown on the y-axis). Closed symbols indicate a significant weighted mean effect size. The open symbol indicates a non-significant weighted mean effect size. The vertical line indicates an effect size equal to zero.

mean being affected by extreme observations. Future assessments of mammal diversity–productivity will be likely to observe an effect similar to what we observed, because the weighted mean effect did not change substantially after 2011. It is unlikely that the mean diversity–productivity relationship will become non-significant.

The studies included in our meta-analysis had a relatively even distribution worldwide (Fig. 1). With the exception of Antarctica (which has no terrestrial mammals), each biogeographical realm was represented by at least four studies. However, no studies were found for both the most and least productive regions in the world. Based on net primary production, the most productive terrestrial regions within each biogeographical realm, such as the Amazon, central Africa, and islands in the Malay Archipelago (Huston & Wolverton 2009), were not represented in our meta-analysis. Arid regions with low productivity (following Huston & Wolverton 2009), such as northern Africa, the Middle East, and Midwest Asia, were also not included in our analysis. Conducting studies in regions that are located in the extreme positions of the productivity gradient could help to develop a more precise understanding of the mammal diversity–productivity relationship worldwide. Filling this spatial gap is a priority, because the most productive regions of the world, such as the Amazon and Central Africa, are rapidly disappearing due to increasing human disturbance so that several species and ecological processes could be lost permanently (Gardner et al. 2009, Hansen et al. 2020).

Policy implications

Globally, a reduction in deforestation rates can be observed from 1980 to 2015, but deforestation is ongoing and is highly heterogeneous across countries: Oceania, central and south Asia, and Latin America have high proportions of lands degraded in historic times compared with Europe and North America (FAO & UNEP 2020). Brazil is a noteworthy case where deforestation rates are increasing after years of consistent decrease (Silva et al. 2020). There are indications that mammalian assemblages are more likely to be able to withstand human anthropogenic disturbance in areas of higher productivity (Peres 2000, Swan et al. 2020). More productive sites, associated with more rapid forest turnover, are usually associated with higher food availability (Phillips et al. 2004) so that ecosystem productivity may lead to increased population sizes and mammal diversity,

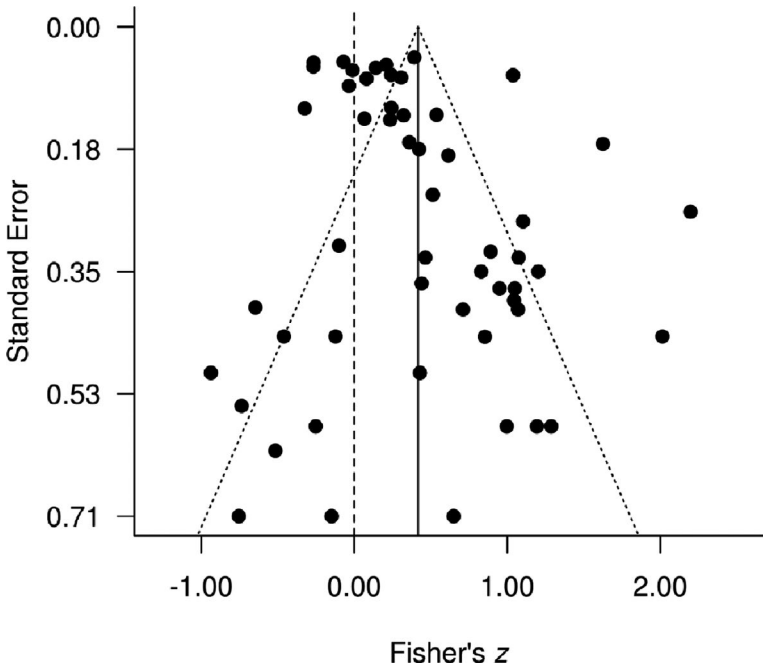

Fig. 5. Funnel plot of the relationship between ecosystem productivity and mammal diversity (Fisher's *z*) and its standard error for each of the 53 studies. The vertical continuous line indicates the weighted mean effect; the vertical dashed line indicates a zero effect. The dotted lines indicate the pseudo-interval of confidence.

and promotes lower extinction rates (Hawkins et al. 2003, Evans et al. 2005, Luo et al. 2012, Gorczynski et al. 2021). Even with increasing anthropogenic activities, the recovery of some groups of mammals can be more rapid in more productive locations, because the higher resource availability and diversity in these locations allow both larger populations and quicker population recovery (Peres & Dolman 2000). As a consequence, species will be less susceptible to local extinctions (Chase 2010), mitigating the impact of anthropogenic disturbance. This has conservation implications, since a higher ecosystem carrying capacity presupposes higher energetic levels to meet the high metabolic requirements of mammals, sustaining more individuals and a more diverse array of species (Hubbell 2001, Allen et al. 2007, Hurlbert & Stegen 2014, Gorczynski et al. 2021). Thus, ecosystem productivity could be assumed to be an ecological factor, which increases environmental resilience to anthropogenic disturbance. Quantifying productivity could help us to identify critical areas for conservation and restoration. Unfortunately, opportunities to study the diversity–productivity relationship are quickly disappearing with the current rate of anthropogenic disturbance. Although productivity is an important ecological factor to consider in mitigating human impact, it is not enough to ensure the protection of the remaining pristine forests. Therefore, we urgently need policymakers and society to commit to implementing strong conservation strategies, in the face of increasing human disturbance.

CONCLUSION

Our results indicate that the diversity–productivity relationship is consistently positive for most groups of mammals; it varies little with the vertical strata explored by the species and feeding guilds, and does not vary with body mass. However, none of the moderator variables we included explained the variation in primary study outcomes. In addition, our results show that productivity is positively correlated with mammal species richness and abundance, but this relationship does not vary with the spatial extent of studies. Animal dispersal capacity and methodological sampling discrepancies could explain part of the variance in the results, because species with limited mobility may have a lower capacity to track changes in productivity (Chase & Leibold 2002). Another possible explanation could be that variance is driven by variation in niche-based and heterogeneity processes (Hamilton et al. 2020), which would lead to variation in resources and could favour the establishment of species with different functional traits. In sum, our findings highlight consistency in the relationship between productivity and mammal diversity.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. List of articles used for analysis of the mammalian diversity–productivity relationship.