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# Species turnover does not rescue biodiversity in fragmented landscapes

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**Thiago Gonçalves-Souza[1,2]✉, Jonathan M. Chase[3,4], Nick M. Haddad[5], Maurício H. Vancine[6], Raphael K. Didham[7,8], Felipe L. P. Melo[9,10], Marcelo A. Aizen[11], Enrico Bernard[12], Adriano G. Chiarello[13], Deborah Faria[14], Heloise Gibb[15], Marcelo G. de Lima[16,17], Luiz F. S. Magnago[18], Eduardo Mariano-Neto[19], André A. Nogueira[20], André Nemésio[21], Marcelo Passamani[22], Bruno X. Pinho[23], Larissa Rocha-Santos[14], Rodolpho C. Rodrigues[24], Nathalia Vieira Hissa Safar[18], Bráulio A. Santos[25], Alejandra Soto-Werschitz[26], Marcelo Tabarelli[7], Marcio Uehara-Prado[27], Heraldo L. Vasconcelos[21], Simone Vieira[28] & Nathan J. Sanders[2]**

Habitat fragmentation generally reduces biodiversity at the patch scale (α diversity)[1]. However, there is ongoing debate about whether such negative effects can be alleviated at the landscape scale (γ diversity) if among-patch diversity (β diversity) increases as a result of fragmentation[2–6]. This controversial view has not been rigorously tested. Here we use a dataset of 4,006 taxa across 37 studies from 6 continents to test the effects of fragmentation on biodiversity across scales by explicitly comparing continuous and fragmented landscapes. We find that fragmented landscapes consistently have both lower α and lower γ diversity. Although fragmented landscapes did tend to have higher β diversity, this did not translate into higher γ diversity. Our findings refute claims that habitat fragmentation can increase biodiversity at landscape scales, and emphasize the need to restore habitat and increase connectivity to minimize biodiversity loss at ever-increasing scales.

Human-induced changes to the biosphere have fundamentally altered biodiversity and ecosystem functioning, and, as a consequence, human well-being[7–9]. Among the many drivers of these changes, habitat loss and reconfiguration due to land-use intensification have been among the most pervasive[1,7–11]. Although there is little doubt that habitat loss typically leads to biodiversity decline[2,12], the consequences of the resulting pattern of habitat fragmentation—one of the most evident outcomes of landscape reconfiguration—are variable and intensely disputed[2–6,13–16].

The controversy with regard to the influence of habitat loss and fragmentation persists for two main reasons. First, the term ‘fragmentation’ refers to a process of habitat loss that can be easily confounded among different variables (for example, habitat patch size, inter-patch isolation, habitat amount and landscape configuration). As a result, it is challenging to synthesize or compare fragmentation studies because they assess the effects of different variables at different spatial scales[2,17]. Second, the definition of fragmentation as a pattern, rather than as a process resulting from habitat loss, suggests to some authors that isolating it from habitat amount (fragmentation per se[18]) is the only way to properly evaluate the effects of fragmentation. Under such an analytical approach, the effects of fragmentation on biodiversity are sometimes, and somewhat controversially, thought to be positive[6,19]. The lack of consensus on how to approach ‘fragmentation’ and the appropriate scale at which to quantify biodiversity have hampered progress on this topic. Until these issues are resolved, consensus about the effects of habitat fragmentation on biodiversity will remain elusive.

Although habitat loss and fragmentation often lead to declines in the number of species that occur locally at the patch scale (α diversity)[20–24], whether and how the effects of fragmentation could lead

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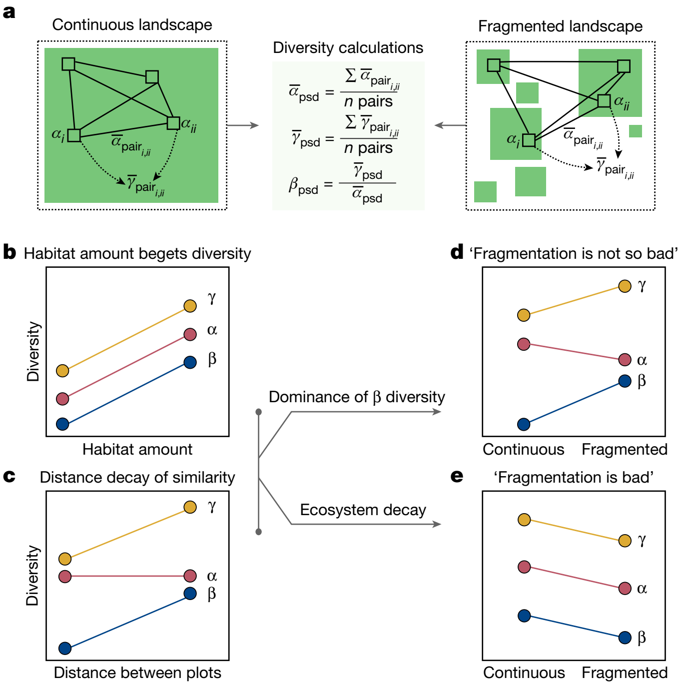
[1]Institute for Global Change Biology, School for Environment and Sustainability, University of Michigan, Ann Arbor, MI, USA. [2]Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA. [3]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany. [4]Institute of Computer Science, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany. [5]Kellogg Biological Station and Department of Integrative Biology, Michigan State University, Hickory Corners, MI, USA. [6]Laboratório de Ecologia Espacial e Conservação Departamento de Biodiversidade, Instituto de Biociências, Universidade Estadual Paulista (Unesp), Rio Claro, Brazil. [7]School of Biological Sciences, University of Western Australia, Perth, Western Australia, Australia. [8]CSIRO Health and Biosecurity, Centre for Environment and Life Sciences, Floreat, Western Australia, Australia. [9]Centro de Biociências, Universidade Federal de Pernambuco, Recife, Brazil. [10]School of Animal, Rural and Environmental Sciences, Nottingham Trent University, Nottingham, UK. [11]Grupo de Ecología de la Polinización (EcoPol), INIBIOMA (CONICET, Universidad Nacional del Comahue), San Carlos de Bariloche, Argentina. [12]Laboratório de Ciência Aplicada à Conservação da Biodiversidade, Departamento de Zoologia, Universidade Federal de Pernambuco, Recife, Brazil. [13]Laboratório de Ecologia e Conservação, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, São Paulo, Brazil. [14]Applied Ecology & Conservation Lab, Universidade Estadual de Santa Cruz, Ilhéus, Brazil. [15]Department of Environment and Genetics, La Trobe University, Melbourne, Victoria, Australia. [16]Center for Large Landscape Conservation, Bozeman, MT, USA. [17]IUCN WCPA Connectivity Conservation Specialist Group (CCPG), Cambridge, UK. [18]Centro de Formação em Ciências Agroflorestais, Universidade Federal do Sul da Bahia, Ilhéus, Brazil. [19]Instituto de Biologia, Universidade Federal da Bahia, Salvador, Brazil. [20]Independent researcher, São Paulo, Brazil. [21]Instituto de Biologia, Universidade Federal de Uberlândia (UFU), Uberlândia, Brazil. [22]Laboratório de Ecologia e Conservação de Mamíferos, Departamento de Ecologia e Conservação, Instituto de Ciências Naturais, Universidade Federal de Lavras, Lavras, Brazil. [23]Institute of Plant Sciences, University of Bern, Bern, Switzerland. [24]Centro Nacional de Pesquisa e Conservação de Aves Silvestres (CEMAVE), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Cabedelo, Brazil. [25]Departamento de Sistemática e Ecologia, Universidade Federal da Paraíba, João Pessoa, Brazil. [26]Laboratorio de Ecología y Diversidad Faunística, Facultad de Ciencias Naturales, Universidad Autónoma de Querétaro, Querétaro, México. [27]Independent researcher, Brasília, Brazil. [28]Núcleo de Estudos e Pesquisas Ambientais, Universidade Estadual de Campinas, Campinas, Brazil. ✉e-mail: tgoncalv@umich.edu



Q12 **Fig. 1 | Habitat amount and distance decay predict different patterns of α, β and γ diversity. a**, Method to calculate pairwise diversity (psd) for α, β and γ using a patch-landscape study design (middle section shows diversity calculations). The dotted line indicates the landscape limits, and the green squares show forest fragments in continuous and fragmented landscapes. Small black squares indicate plots in which species were sampled, and each continuous line connecting two squares represents all potential pairs to be compared. **b**, Habitat amount begets diversity by increasing patch α diversity and landscape γ diversity, altering composition between patches (β diversity). **c**, Distance decay of similarity predicts that β diversity increases with the distance between plots. Because increasing distance also samples from a larger regional pool, it can increase γ diversity. However, there is no a priori expectation that distance affects α diversity; therefore, it remains unchanged if we assume no specific directional gradient. By combining predictions from habitat amount and distance decay (middle arrows), we can test whether the 'dominance of β diversity' or the 'ecosystem decay' hypothesis better explains changes in α, β and γ diversity between continuous and fragmented landscapes. Two possible conceptual scenarios emerge when accounting for habitat amount and spatial distance to test the effects of fragmentation on biodiversity. **d**, The 'fragmentation is not so bad' hypothesis suggests that increasing heterogeneity between fragments boosts β diversity, consequently increasing γ diversity. **e**, The 'fragmentation is bad' hypothesis posits that fragmentation negatively affects all biodiversity metrics, even when controlling for habitat amount.

to changes at the landscape scale (γ diversity) is still debated[19,23,25,26]. Specifically, how changes in α diversity translate into changes in γ diversity depends crucially on the magnitude and drivers of compositional turnover among communities in the remaining fragments (that is, β diversity)[3,27]. If landscape-scale β diversity is naturally high, the effects of fragmentation on γ diversity might be minimized[15,28]; in cases of augmented β diversity, fragmentation could increase γ diversity, even if α diversity decreases (the 'dominance of β diversity' hypothesis[3,29]). For example, dispersal limitation among isolated fragments and increasing environmental heterogeneity could enhance landscape-scale β diversity in fragmented landscapes[3,30,31] (Fig. 1). By contrast, communities in fragmented landscapes could also exhibit lower β diversity if, for example, common disturbance-adapted or generalist species persist in fragments, whereas rare habitat specialists are extirpated[32,33].

The central features of the debate about the effects of habitat fragmentation on α, β and γ diversity have important implications for conservation and can inform decisions about optimal landscape configuration for maintaining or even maximizing biodiversity[5,13,14,28]. If landscape-scale γ diversity is maintained in increasingly fragmented landscapes because β diversity is high, one could argue that conserving several small, isolated fragments enhances conservation of biodiversity[34,35]. Such a strategy would conserve biodiversity if, and only if, β diversity effectively rescues γ diversity in the face of declining patch-scale α diversity (Fig. 1). Several attempts have been made to identify the scale and relevant variables that determine whether and how habitat fragmentation shapes α, β and γ diversity[4,6,11,25,36]. However, it remains unclear whether the putative rescue of γ diversity by increased β diversity in fragmented landscapes has a generalizable mechanistic basis or is due purely to geometric artefacts (that is, increased geographical distance among remnants; Supplementary Text 1).

Here, we use a dataset that includes 4,006 species (33 amphibians and reptiles, 162 birds, 227 mammals, 1,859 invertebrates and 1,725 plants) taken from 37 landscapes distributed across 6 continents (Supplementary Text 2 and Extended Data Figs. 1 and 2) to examine the effects of forest fragmentation on α and γ diversity, as mediated by changes in β diversity. We evaluated scenarios under which fragmentation would increase (the 'fragmentation is not so bad' hypothesis[6]) or decrease ('fragmentation is bad' hypothesis[4]) landscape-scale biodiversity (γ diversity) (Fig. 1). The data we analyse permit a paired comparison of multiple samples taken from a very large fragment (often called 'continuous forest' and referred to here as 'continuous landscape') (1,000–300,000 ha) as a direct control for comparisons with samples taken from several smaller fragments in the adjacent fragmented landscape. These fragmented landscapes tend to have lower habitat Q13 amounts and lower patch and edge densities than do adjacent continuous landscapes (Extended Data Figs. 3–5). We also accounted for the spatial distance between fragments and differences in sampling effort within and among studies to calculate α, β and γ diversity. Finally, we included habitat amount (estimated as the percentage of forest cover in concentric buffers) in statistical models to understand the relative roles of fragmentation and habitat loss on α, β and γ diversity.

Across taxa and study systems, we found that α diversity was consistently lower in fragmented landscapes relative to α diversity in the adjacent continuous landscapes (Fig. 2 and Extended Data Fig. 6). These negative effects of fragmentation on α diversity persisted when we controlled for several confounding factors (Supplementary Tables 1–6), including the number of fragments sampled (Fig. 2a), the distance between fragments (Fig. 2b) and the sampling effort (Fig. 3). Independent of the method, α diversity decreased, on average, by 13.6% (range, 11.8–19.7%) when comparing continuous with fragmented landscapes. When we used diversity metrics that differentially weight rare versus abundant species (the effective number of species[37]), α diversity was still lower in fragmented landscapes than in adjacent continuous landscapes, regardless of the weighting applied (Fig. 3a,b and Extended Data Fig. 6). Thus, the decline of α diversity in fragmented landscapes occurs when considering both rare and abundant species (Fig. 3). Variation among studies in how habitat amount differed between continuous versus fragmented landscapes did not explain the consistent loss of α diversity in fragmented landscapes (Supplementary Tables 1–6). These negative effects on α diversity are largely consistent with other studies[2,38], leaving little doubt (or perhaps even a consensus) that fragmentation of terrestrial habitats reduces patch-scale α diversity.

Fragmented landscapes also had lower landscape-scale γ diversity: there were, on average, 12.1% fewer species (range, 10.7–18%) in the fragmented landscapes relative to the adjacent continuous landscapes (Fig. 2 and Extended Data Fig. 6). Similarly to α diversity, γ diversity remained lower in fragmented landscapes even when we controlled for potential confounding effects due to underlying distance decay of similarity (Fig. 2b) and used diversity metrics that varied in their relative weighting of rare versus abundant species (Fig. 3a,b and Extended Data Fig. 6). As a result, our global synthesis shows that the negative effects of habitat

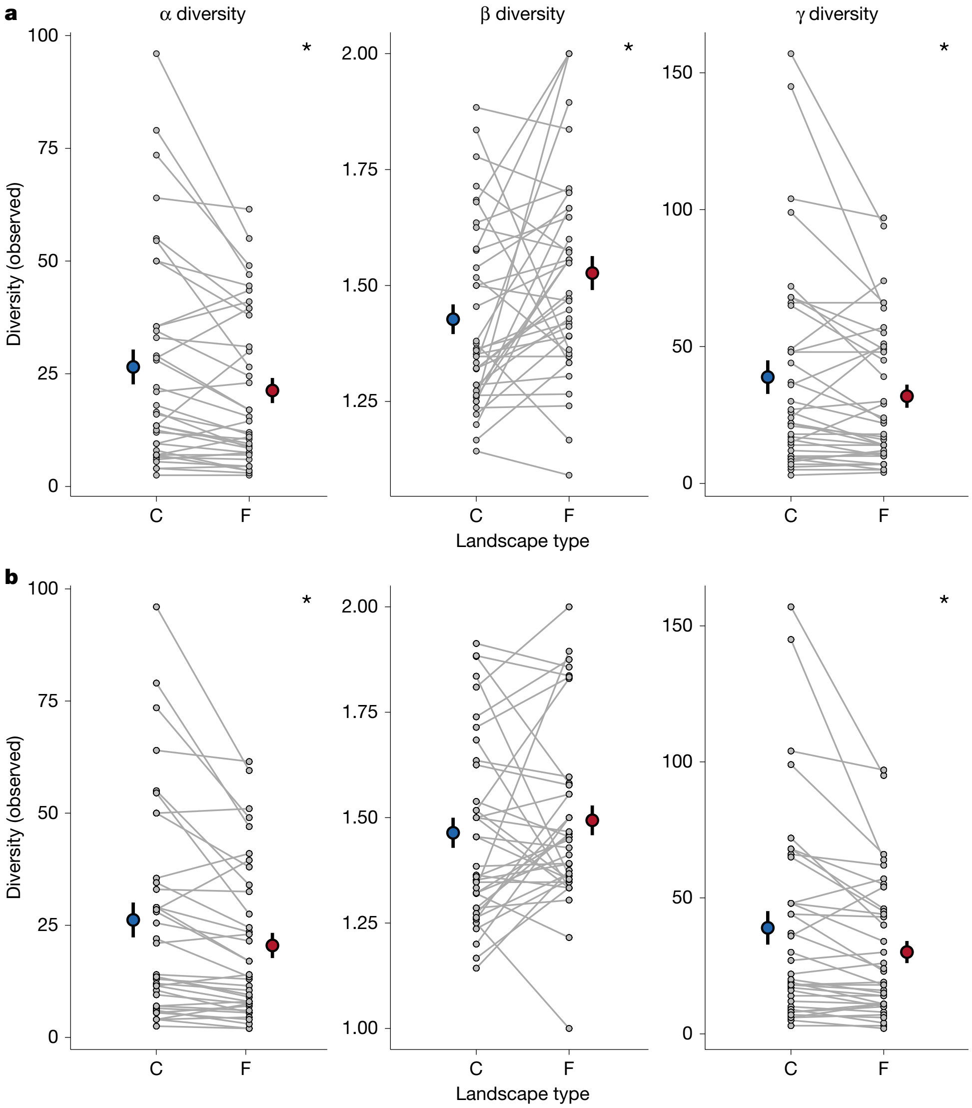


**Fig. 2 | Differences in α, β and γ diversity in continuous and fragmented landscapes. a**,**b**, The values of α, β, and γ diversity were computed using all possible plot pairs (**a**) or only the nearest plot pairs (controlling for distance decay effects) (**b**) in both continuous (C) and fragmented (F) landscapes. The pairwise sample diversity metric controls for differences in the number of plots between continuous and fragmented landscapes, enabling comparisons across studies. Large circles represent the mean of α, β and γ diversity in fragmented (red circles) and continuous (blue circles) landscapes across studies. Error bars represent standard error. Small grey circles represent observed diversity values per study ($n = 37$), and the line connects the two landscape types from the same study. Asterisks indicate significant differences ($P < 0.05$) in generalized linear mixed models (GLMMs) (*$P < 0.05$; Supplementary Tables 1–6) and meta-analyses (Supplementary Tables 8–13).

loss and fragmentation on α diversity are not fully mitigated (nor do they show evidence of being positive) at the landscape scale (γ diversity). Notably, unlike other studies that found that β diversity compensated for losses in α diversity by increasing γ diversity[3,35,39], our synthesis of fragmentation studies appropriately controls for variation in study design, sampling effort and distance among fragments. The lower α and γ diversity in fragmented landscapes relative to continuous landscapes was correlated with underlying differences in habitat amount between landscape types, but the effects of fragmentation remained significant after accounting for variation in habitat amount (Supplementary Tables 1–6), and the relative importance of landscape type (continuous or fragmented) was a stronger factor (Extended Data Fig. 7). This suggests that, in addition to the effects of reduced habitat amount, fragmentation and other degradation processes (for example, edge effects[40]) have a key role in the loss of biodiversity at both the patch and the landscape scale. This result was robust when using alternative analytical approaches (Extended Data Fig. 6 and Supplementary Tables 8–13).

Logically, for previous claims to hold true that fragmentation has minimal effects on γ diversity (or even increases it), declines in α diversity would have to be offset by large increases in β diversity among fragments. That is, the communities remaining in the fragments would have to become increasingly dissimilar to one another[3,34,39,41]. Certainly, we did find higher β diversity in fragmented landscapes than in adjacent continuous landscapes (Fig. 2a and Extended Data Fig. 6), irrespective of the β diversity metric used (Supplementary Text 3). This pattern is to be expected on the basis of geometric effects alone, given that sampling locations in fragments were, on average, 22% farther apart than were sampling points within the continuous forested landscapes in our global synthesis (that is, distance decay of similarity[42,43]). However, this observed increase in β diversity in fragmented landscapes completely disappeared when we accounted for the underlying distance-decay effect by comparing only adjacent fragments in each study (Fig. 2b). Thus, any positive effect of fragmentation on β diversity arises only when fragments are considerably distant from one another. How far

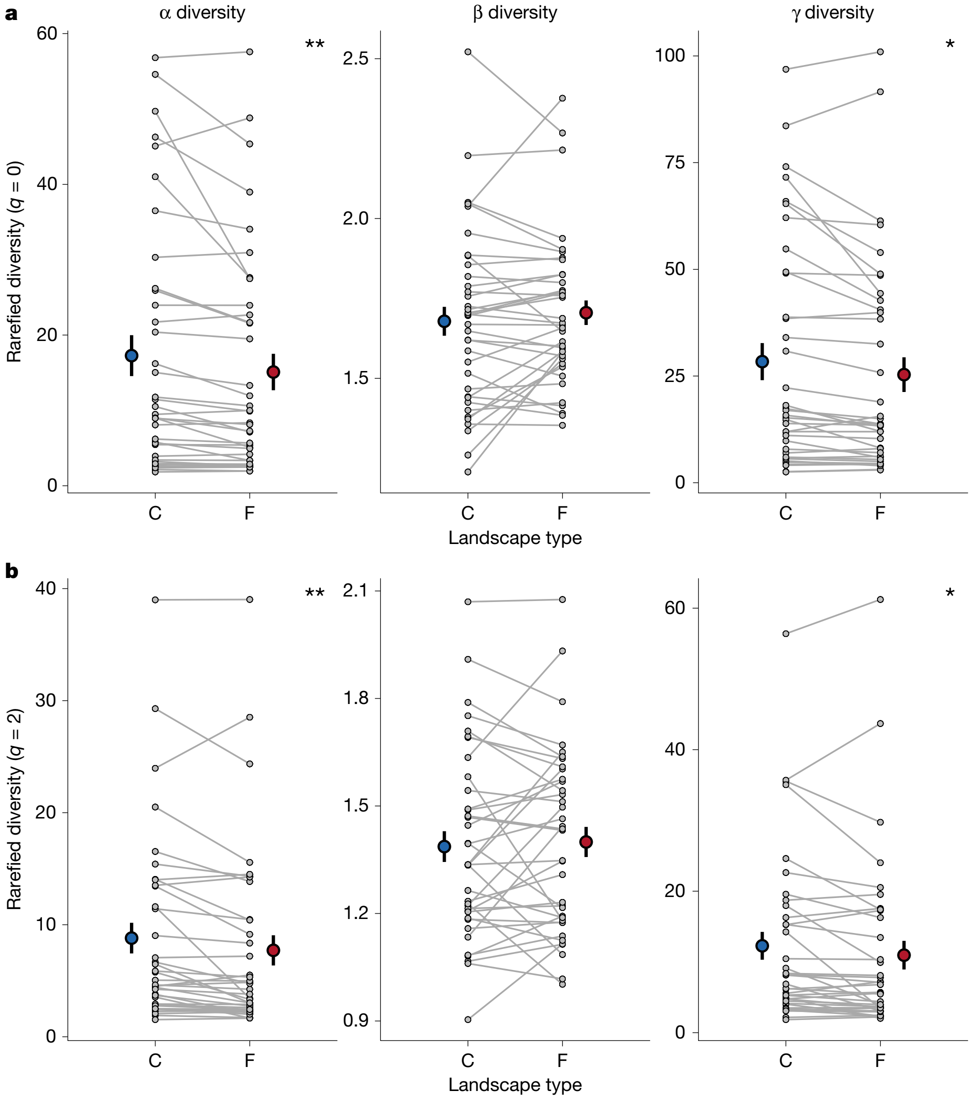


**Fig. 3 | Differences in α, β and γ diversity in continuous and fragmented landscapes controlling for differences in sampling effort and using all plot pairs. a**,**b**, Rarefied α, β and γ diversity giving greater relative weight to rare ($q = 0$) (**a**) or abundant ($q = 2$) (**b**) species. Large circles represent the mean of the rarefied α, β and γ diversity in fragmented (red circles) and continuous (blue circles) landscapes across studies, and error bars represent standard error. Small grey circles represent the observed rarefied diversity per study ($n = 37$), and the line connects the two landscape types from the same study. Asterisks indicate significant differences ($P < 0.05$) in GLMMs (**$P < 0.001$, *$P < 0.05$; Supplementary Tables 1–6) and meta-analyses (Supplementary Tables 8–13).

apart they need to be to increase β diversity probably varies among taxa and depends on dispersal ability. This result challenges the generality of the dominance of β diversity hypothesis, which has received some support in studies of tropical regions[29,44,45]. Even in studies that provide some support for the dominance of β diversity hypothesis, it remains unclear whether the increase in β diversity in fragmented landscapes occurs solely because of the confounding effect of increasing distance among fragments or other factors (Supplementary Text 1). Consequently, separating fragmentation-related and pure distance effects on β diversity is essential to understanding the processes that determine biodiversity change at the landscape scale. Future studies might investigate how changes in β diversity that result from distance decay are driven by dispersal limitation, increasing habitat heterogeneity or other processes.

In addition to influencing the numbers of species, habitat loss and fragmentation can also affect which species occur and persist in smaller and more isolated fragments compared with more continuous habitats[32,38]. To understand whether habitat loss and fragmentation led to changes in community composition in fragmented landscapes, we analysed community compositional changes between fragmented and continuous landscapes, and tested whether these changes were associated with species turnover (compositional changes between fragmented and continuous landscapes) or nestedness (in which species from fragmented landscapes represent a subset of those species in the continuous landscape). We found that species turnover is moderately more important than nestedness, accounting for 53% of the total dissimilarity between continuous and fragmented landscapes (Supplementary Text 3). Thus, communities in fragmented landscapes are expected to retain only a fraction of those species that occur in continuous habitats, also suggesting that many of the species persisting in fragmented forests are opportunistic species that thrive in the surrounding matrix.

Our results bring new evidence in a debate that has permeated the literature on fragmentation for the past five decades[4–6,13,14,46]. First, consistent with the theory of island biogeography, habitat loss and fragmentation often reduce connectivity in ways that should reduce α diversity, especially in extremely degraded landscapes[13,47,48]. Declines in α diversity could be driven by losses in habitat amount and quality[49]. Owing to data limitations, we could not explicitly examine whether habitat quality influenced α diversity, but we did show that patch-scale α diversity is indeed lower in fragmented landscapes than in continuous landscapes[19,50]. Second, as distance between fragments increases, the compositional similarity between those fragments should decrease[38], which our global synthesis corroborates. Indeed, our synthesis unites these two processes—habitat loss and fragmentation both reduce α diversity and increased distances between fragments increases β diversity. However, when confounding factors such as distance decay and sampling effort are controlled, the claim that increasing β diversity buffers the loss of α diversity by preserving diversity at larger scales[34] does not hold. Put simply, fragmented landscapes have lower diversity, at all scales, than do unfragmented landscapes.

Our main finding is that increases in β diversity in fragmented landscapes do not buffer losses of α diversity or rescue fragmented landscapes from losses of γ diversity. Instead, β diversity increases within fragmented landscapes only when inter-patch distance is high. The higher γ diversity in continuous landscapes reinforces the need to protect large forest areas to safeguard biodiversity conservation. Our synthesis shows that as habitats continue to be degraded, altered, reduced and fragmented, biodiversity at local and landscape scales is lost. The pervasive effects of ongoing habitat destruction and fragmentation are real and should not be minimized. Although many species can sometimes persist in small fragments, conservation efforts and policies should seek to prevent fragmentation and habitat alteration and focus on connecting what are often increasingly isolated fragments.

## Online content

Any methods, additional references, Nature Portfolio reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at https://doi.org/10.1038/s41586-025-08688-7.

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# Methods

## Dataset

Q14 LandFrag[51] is an open dataset that is a compilation of species abundance distributions across forest fragments for vertebrates, invertebrates and plants from 121 studies around the world. For a study to be included in the dataset, it had to provide information about species abundances and identities per forest fragment, and consist of samples in more than four fragments with geographical coordinates (more details in a previous study[51]). Most of these geographical regions have experienced intense habitat destruction: the mean fragment size across all studies is 305 ha (±267 ha s.d.), 67% of all studied fragments have an area less than 100 ha and 12.5% of continuous landscapes have an area larger than 1,000 ha. Studies occurred on every continent except Antarctica, but 64% of the studied regions with larger fragments were located in South America, particularly Brazil, where habitat fragmentation is most rapid (Extended Data Fig. 2). We selected a subset of 37 of the 121 studies that sampled organisms in multiple fragments in both continuous and fragmented landscapes with multiple fragments (Extended Data Fig. 1). These 37 studies use a 'patch-landscape' design (as defined previously[52]), in which the numbers of individuals and species were measured in a focal large forest or fragment, but the predictors represent variables measured at the landscape scale (Supplementary Text 4). These inclusion criteria excluded many datasets without intact forests or large fragments in continuous landscapes (Supplementary Text 2).

## Scale and landscape-type definition

The definition of continuous landscapes was based on the authors' descriptions, in which they referred to the patch as a 'continuous forest' without estimating its actual area; this characterization applied to 9 out of 37 studies. Moreover, because some habitat loss and fragmentation studies sample either the largest fragment or the most contiguous forest as a 'control' fragment to measure biodiversity changes in human-altered landscapes, we included these as representations of the 'continuous landscape' (28 out of 37 studies). The number of large or continuous forests varied across studies, with some including more than one large forest (Supplementary Table 7). Therefore, the continuous landscape can be represented either by a single large, continuous forest or by multiple large forests interspersed with several small fragments. The average size of the largest forests in these 28 studies is 30,908 ha (minimum, 1,000 ha; maximum, 300,000 ha), whereas the average size for fragments is 148 ha (minimum, 5.8 ha; maximum, 1,094 ha). On average, large fragments in continuous landscapes are 157 times larger than small fragments in fragmented landscapes, with this ratio ranging from 4.62 times to 10,169 times. For studies that categorized the continuous landscape as a 'continuous forest', the average size of the small fragments is 55.96 ha (minimum, 0.51 ha; maximum, 99.86 ha) (more details in Supplementary Table 7).

We calculated the following landscape variables to compare each landscape type (continuous and fragmented): (i) percentage of forest cover (that is, habitat amount; Extended Data Fig. 3) and (ii) number of patches (Extended Data Fig. 4). We also compared the number of patches, patch density, edge density and mean perimeter–area ratio between continuous and fragmented landscapes considering different habitat amount classes (Supplementary Text 4 and Extended Data Fig. 5). Although forest cover quantifies the amount of habitat (that is, landscape composition), the number of patches, patch density, edge density and Euclidean nearest-neighbour distance are variables that describe landscape configuration (that is, habitat fragmentation)[53].

We defined $\alpha$ diversity as the number of species in a given patch (patch-scale diversity). The landscape-scale diversity ($\gamma$ diversity), in turn, represents the number of species in all patches, for multiple landscapes in a given study. $\beta$ diversity is then calculated as the compositional changes between patches from multiple landscapes in a given study. Below, we describe four standardization procedures we used to ensure robust estimates of $\alpha$, $\beta$, and $\gamma$ diversity across all studied sites.

## Standardizing $\alpha$, $\beta$ and $\gamma$ diversity

There are challenges in comparing continuous and fragmented landscapes within and between studies, including potentially confounding differences in (i) study design, (ii) sampling effort and number of species, (iii) distance between patches and (iv) habitat amount. Moreover, these datasets included various taxonomic groups, from insects and arachnids to mammals and plants, sampled by several methods. Because of this, we were not able to identify a subset of studies that all used the same sampling methodology (for example, pitfall traps as opposed to active sampling), even within the same taxonomic group[50]. Thus, we decided to use all studies and to run different standardization strategies accounting for different confounding factors, as described in the analysis pipeline (Extended Data Fig. 8) and the subsections below.

**Consider study design for estimating $\alpha$ diversity.** To standardize Q15 comparisons between continuous landscapes and neighbouring fragments, we computed patch-scale $\alpha$ diversity while accounting for differences in sampling design and sampling effort[50]. Specifically, there are two notable sampling discrepancies that affect the number of sampled individuals in fragmentation research. First, most studies sample organisms in more fragments than in continuous landscapes, with the latter typically represented by a single large forest fragment. Second, both continuous forests and bigger fragments generally contain more plots than do smaller fragments. Therefore, the number of sampled individuals will vary between fragments with different sizes and between continuous and fragmented landscapes.

We standardized comparisons between continuous and fragmented landscapes by using three approaches that estimate $\alpha$ diversity components at the patch scale. We first categorized study designs in three categories: (i) standardized sample ($n = 8$), (ii) standardized subsample ($n = 16$) and (iii) pooled samples ($n = 13$), as defined previously[50]. The standardized sample included studies that used the same number of samples among fragmented and continuous landscapes. Standardized subsamples, in turn, included those studies that used an unequal sample size (higher intensity in larger fragments and in continuous forests), but species abundance and composition were available for each sampling unit. Pooled samples represented studies with unequal sampling effort that combined all samples per fragmented or continuous landscape without providing per-sample species abundances. To standardize the studies in sample designs (i) and (ii), we calculated the average number of individuals per sampling unit ($N_{\mathrm{std}}$). For the sample design (iii), we used information about sampling intensity to calculate $N_{\mathrm{std}}$ on the basis of the relative sampling effort ($\mathrm{SAMP}_{\mathrm{rel}}$) per fragment. $\mathrm{SAMP}_{\mathrm{rel}}$ was defined as the sampling effort in a fragment divided by the minimum sampling effort in all fragments of a study[50]. Then, $N_{\mathrm{std}}$ was calculated as the observed number of individuals ($N_{\mathrm{obs}}$) divided by $\mathrm{SAMP}_{\mathrm{rel}}$.

**Standardize $\alpha$ diversity by sampling effort.** Studies comparing species richness between continuous and fragmented landscapes usually have samples taken at different efforts to account for variation in patch sizes[4]. Because of that, we estimated the standardized number of species ($\alpha_{\mathrm{std}}$) on the basis of a consistent sampling effort $N_{\mathrm{std}}$[50]. Whereas $\alpha_{\mathrm{std}}$ was calculated as the observed number of species in $N_{\mathrm{std}}$ for sample designs (i) and (ii), we used individual-based rarefaction[54] for sample design (iii) to calculate $\alpha_{\mathrm{std}}$ based on the fragment with the smallest $N_{\mathrm{std}}$ in a study, using the R package iNEXT[7,55]. Q16

**Standardize $\beta$ and $\gamma$ diversity by sampling effort.** Although the standardization of $\alpha$ diversity on the basis of different sampling designs is possible and allows for fair estimation of patch-scale diversity[50], the same cannot be said for $\beta$ and $\gamma$ diversity. First, as mentioned above, the number of sampled plots is usually higher in fragments than in continuous landscapes, which affects the calculation of γ diversity. Second, if we compare two studies with different numbers of fragments or plots, or a study on mammals with another on beetles, γ diversity can be significantly influenced by differences in the size of the species pool. We controlled for the number of fragments or plots by estimating the average 'pairwise sample diversity' (hereafter, psd), as recommended Q17 previously[56]. This method represents the calculation of α, β and γ diversity for a pair of fragments or plots (Extended Data Fig. 9). It uses the mean and pooled values of standardized patch-scale diversities ($\alpha_{std}$) to calculate $\overline{\alpha}_{pair}$ and $\overline{\gamma}_{pair}$ diversity, respectively, for every pair of fragments or plots (Extended Data Fig. 9a). Subsequently, after calculating the $\overline{\alpha}_{pair}$ and $\overline{\gamma}_{pair}$ for all possible pairs in each landscape type, we calculated $\overline{\alpha}_{psd}$ and $\overline{\gamma}_{psd}$ by dividing the sum of all $\overline{\alpha}_{pair}$ and $\overline{\gamma}_{pair}$ by the total number of pairs (Extended Data Fig. 9b) or by the number of nearest pairs only (controlling for distance decay; Extended Data Fig. 9c). The value of $\overline{\beta}_{psd}$ was then derived using Whittaker's multiplicative beta diversity ($\overline{\beta}_{psd} = \overline{\gamma}_{psd}/\overline{\alpha}_{psd}$). For completeness, we also calculated β diversity using Jaccard ($\beta_J$), Sorensen ($\beta_S$) and Bray–Curtis ($\beta_{BC}$) indices to ensure that the choice of the index would not affect our conclusions. We found these indices to be correlated strongly with one another and therefore we use only Whittaker's $\overline{\beta}_{psd}$ in the analyses (Supplementary Text 3).

Furthermore, we used individual-based rarefaction[54,55] to estimate the number of species per fragment or plot pair on the basis of the same sampling sample size or abundance. First, we used the fragment or plot with the smallest number of individuals to estimate the rarefied number of species per plot or fragment ($\overline{\alpha}_{rarefied}$) and the mean rarefied pairwise sample diversity ($\overline{\alpha}_{psd\_rarefied}$). Second, we selected all possible pairs per fragment or plot per study and summed the number of individuals in those pairs. We then used the pair with the smallest number of individuals as the baseline to estimate the rarefied number of species per pair ($\overline{\gamma}_{psd\_rarefied}$). Likewise, ($\overline{\beta}_{psd\_rarefied}$) was estimated by dividing $\overline{\gamma}_{psd\_rarefied}/\overline{\alpha}_{psd\_rarefied}$. To estimate α, β and γ diversity in the above rarefaction analyses, we used two Hill numbers: $q = 0$, which quantifies species richness irrespective of species relative abundances, therefore giving greater relative weight to rare species (Fig. 3); and $q = 2$, which gives greater relative weight to abundant species (that is, Simpson index; Fig. 3). We also compared diversity values obtained from individual-based rarefaction with coverage-based rarefaction and the results were highly correlated ($r > 0.95$). Therefore, we decided to use only individual-based rarefaction.

**Accounting for the confounding effects of distance decay on α, β and γ diversity.** Comparing species diversity in multiple plots or fragments dispersed across the landscape can be confounded by variation in spatial extent between landscape types, because more distant plots would always be expected to be more dissimilar to one another even before landscape modification ('distance decay of similarity'; Supplementary Text 2). In fact, the average distance between fragments is 22% larger (mean, 23.8 km) than the distance between plots within the continuous forest (mean, 19.4 km). Therefore, alterations in β diversity might stem from distance decay of similarity[42,43], rather than from a response to habitat heterogeneity or other patch or landscape-scale variables. Thus, we accounted for underlying distance decay effects on α, β and γ diversity by considering only the nearest neighbour fragments in fragmented landscapes or nearest plots (or forests) in the continuous landscapes (Extended Data Fig. 9c). We calculated the diversity of the nearest pairs using the same approach as that described above (paired diversity, and paired individual-based rarefied diversity). However, instead of selecting all pairs within each landscape type per study, we used only pairs that represented one focal fragment (or plot in continuous landscape) and the nearest fragment (or plot) (Extended Data Fig. 9c).

**Accounting for variation in habitat amount.** One potential problem in inferring that changes in habitat configuration drive differences in diversity between continuous and fragmented landscapes is that habitat amount is likely to co-vary with landscape type (Supplementary Text 4, Supplementary Tables 1–6 and Extended Data Fig. 5). Consequently, we tested whether any changes in diversity between continuous and fragmented landscapes remained significant, after accounting for intrinsic underlying differences in habitat amount between landscape types. To quantify habitat amount, we generated concentric buffers around each plot, with radii of 200 m to 2,000 m, in 200-m increments. Within each buffer, the percentage of forest was estimated to represent the habitat amount. We then established the average habitat amount as the mean value across all plots, for each buffer radius, as the predictor variables for use in statistical analyses (for more details about the extraction of landscape variables, see ref. 51).

## Statistical analyses

Because the underlying amount of habitat can vary between the two landscape types (Extended Data Fig. 3), we use models that test for the effects of fragmentation on diversity after accounting for differences that might be expected between landscape types solely as a function of variation in habitat amount[12] (more details in Supplementary Text 4). There is no single statistical approach that can overcome the inherent multicollinearity of habitat amount and configuration effects in observational landscape studies, so we use three approaches to gain a consensus understanding of the relative importance of fragmentation effects: variance component approach, model averaging approach and meta-analytic approach.

**Variance component approach.** We used generalized linear mixed models (GLMMs) (with Gaussian family and the R package glmmTMB[57]) to compare diversity differences (α, β and γ diversity) between landscape types (fragmented and continuous). Landscape type was treated as a fixed factor, and study as a random factor. We first built a simple model to test whether α, β and γ diversity differ between landscape types: Q18

model1 = glmmTMB(diversity ~ landscape type + (1|study))

We then tested the assumptions of residual normality, variance homogeneity, and over- or underdispersion with the R package DHARMa[58], and log-transformed response variables that did not satisfy these assumptions. In the second model, we included habitat amount and study as random factors:

model2 = glmmTMB(diversity ~ landscape type + (habitat amount|study))

This model includes a random slope for habitat amount within each study with random intercepts, allowing the effects of habitat amount on diversity to vary across studies.

Next, we extracted the slopes from model 2 using the function ranef.glmmTMB (ref. 57) to further investigate whether other moderators can explain the variation in α, β and γ diversity using linear models. For these linear models, we reported the estimates and the lower and upper 95% confidence intervals for each moderator (Supplementary Tables 1–6). These moderators include confounding variables such as habitat amount, time since fragmentation, number of fragment pairs and clustering of studies in South America, which might explain diversity changes.

We first classified studies on the basis of habitat amount, defined Q19 into one quantile, with two equal-spaced probabilities splitting the data into two extremes: degraded regions with habitat amounts ranging from 34.5% to 65.8%; and conserved regions with habitat amounts ranging from 65.8% to 98.4%. To define time since fragmentation, we considered the estimated time a given landscape was first fragmented. Because this information is rarely available in the published papers, we created two categories representing this time frame: intermediate (between 20 and 100 years) and long (more than 100 years). There were no studies in which fragmentation occurred fewer than 20 years ago.

Although we used rarefaction methods to standardize diversity comparisons on the basis of sampling effort and sample size, the number of pairs to calculate diversity will differ between landscape types. Therefore, we used the number of fragments or plot pairs as moderators. Furthermore, there is an uneven geographical distribution of fragmentation studies, with most of them focused on the global south (see more details in Supplementary Text 2). The clustering of studies, particularly in South America, could be considered a limitation of our study, but we addressed it by including a categorical variable (South America versus other continents) as a moderator in the model. The DHARMa diagnostics showed that all models (with or without log transformation) satisfy all GLMM assumptions. In the main analyses, we used the average habitat amount for the buffer of 2,000-m radii.

**Model averaging approach.** We also used a model averaging approach[59] to test the relative importance of habitat amount and landscape type. In this approach, we considered habitat amount and landscape type as fixed variables, allowing us to directly compare their effects on diversity. Because there is a correlation between landscape type and habitat amount (Extended Data Fig. 3), we did not use the common Akaike information criterion and related methods (AIC, AICc and delta), because they are affected by correlation between predictors[59]. Instead, we used a previously described approach[59] to calculate partial standard deviations, *t* statistics and AICc weights based on standardized estimates. We created three models:

model3 = glmmTMB(diversity ~ landscape type
+habitat amount + (1|study))

model4 = glmmTMB(diversity ~ landscape type + (1|study))

model5 = glmmTMB(diversity ~ habitat amount + (1|study))

As recommended previously[59], habitat amount was centred for better interpretation of the predictors. First, we calculated the partial standard deviations using models 3, 4 and 5 to handle multicollinearity when estimating the AICc weights. We then standardized the parameter estimates using these partial standard deviations. Moreover, we calculated the ratio of absolute values of the *t* statistics to provide unbiased estimates of the relative importance of individual predictors[59]. Next, we used the standardized coefficients (estimated with the partial standard deviations) to calculate the unbiased AICc weights. These weights were then multiplied by the scaled importance (estimated from the *t* statistics) to determine the individual contributions of habitat amount and landscape type.

**Meta-analytic approach.** As described above and in Supplementary Text 4, it is challenging to tease apart the effects of habitat fragmentation on diversity with this paired design based on observational data. In addition to the GLMMs used above, we also performed mixed-effects meta-analyses using the function rma.uni from the metafor R package[60]. The meta-analyses can allow explicit inclusion of habitat amount as a quantitative moderator explaining diversity changes between continuous and fragmented landscapes. We calculated the effect size using the log-response ratio (LRR) comparing α, β and γ diversity between landscape types. The LRR calculates the proportional changes in the average diversity between two groups:

$$\mathrm{LRR} = \log(\mathrm{Diversity_c}/\mathrm{Diversity_f})$$

where $\mathrm{Diversity_c}$ is the average diversity in the continuous landscape, and $\mathrm{Diversity_f}$ is the average diversity in the fragmented landscape. Positive LRR values indicate that continuous landscapes have higher diversity than fragmented landscapes, whereas negative LRR values show that fragmented landscapes have higher diversity. Because the average diversity is obtained from the pairwise diversity described above, we can estimate the standard deviation and sample size (number of fragment or plot pairs) and then calculate the variance of the LRR:

$$\mathrm{LRR_{var}} = \frac{(\mathrm{SD_c})^2}{\mathrm{N_c Diversity_c^2}} + \frac{(\mathrm{SD_f})^2}{\mathrm{N_f Diversity_f^2}}$$

where $\mathrm{SD_c}$ and $\mathrm{SD_f}$ represent the standard deviations of continuous and fragmented landscapes, respectively, and $N_c$ and $N_f$ represent the number of plot pairs in continuous and fragmented landscapes, respectively. We calculated the LRR and its variance for all measures of diversity described above: α, β and γ diversity using all plot pairs and the nearest pairs (accounting for distance decay). Furthermore, we also calculated the LRR using the rarefied estimates of α, β and γ diversity in scenarios with all or nearest plot pairs. By doing this, we calculated the LRR for all 37 studies using different methods accounting for sampling effort and spatial distance.

We fitted mixed-effects meta-analyses with a restricted maximum likelihood estimator to compare the overall LRR among studies. This overall analysis tests whether the LRR is different from zero (indicating no difference between fragmented and continuous landscapes) and compares the heterogeneity in the random term effects, treating each study as a random effect. In addition, we tested whether other moderators could explain the variation in the effect sizes. When comparing continuous and fragmented landscapes, habitat amount is a relevant covariate, because fragmented landscapes tend to have less habitat (Supplementary Text 4). Therefore, we included habitat amount as a moderator using two different strategies. First, we calculated the average habitat amount across studies, disregarding the landscape type, to split the studies into regions with different levels of degradation. To do this, we divided the data into two categories as described above: (i) degraded regions with habitat amounts varying from 34.5% to 66%; and (ii) conserved regions with habitat amounts varying between 66% and 98.4%. We then used this categorical moderator in the mixed-effects meta-regression. Second, as we mentioned above, we might expect that differences in habitat amounts between landscape types have a greater influence on diversity in fragmented than in continuous landscapes. Therefore, we compared the average habitat amount (HA) in continuous ($\mathrm{HA_c}$) and fragmented ($\mathrm{HA_f}$) landscapes by calculating the habitat amount difference ($\mathrm{HA_D}$) = $\mathrm{HA_c} - \mathrm{HA_f}$. Then, we used $\mathrm{HA_D}$ as a continuous moderator in a mixed-effects meta-regression. Finally, we added a categorical moderator comparing South America with other continents to investigate whether South America (the region with the most studies) can explain the variation in the effect sizes (Extended Data Fig. 10). We further tested how different sources of heterogeneity might affect the results by performing various sensitivity analyses (Supplementary Text 5).

### Inclusion and ethics

All authors are committed to upholding the principles of research ethics and inclusion as advocated by the Nature Portfolio journals. All local partners who contributed their datasets have been included as co-authors.

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

## Data availability

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The datasets used in this paper are available at GitHub (https://github.com/thiago-goncalves-souza/ms-biodiversity-loss-fragmented-landscapes).

## Code availability

The code used in this paper is available at GitHub (https://github.com/thiago-goncalves-souza/ms-biodiversity-loss-fragmented-landscapes).

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**Author contributions** T.G.-S., J.M.C., N.M.H. and N.J.S. conceived and designed the study. T.G.-S. performed the analyses with support from J.M.C., N.M.H., N.J.S., M.H.V. and F.L.P.M. T.G.-S., J.M.C., N.M.H. and N.J.S. wrote the first version of the paper. F.L.P.M., M.A.A., E.B., A.G.C., R.K.D., D.F., H.G., M.G.d.L., L.F.S.M., E.M.-N., A.A.N., A.N., M.P., B.X.P., L.R.-S., R.C.R., N.V.H.S., B.A.S., A.S.-W., M.T., M.U.-P., H.L.V. and S.V. collected data. J.M.C., T.G.-S. and M.H.V. curated and maintained the data. All authors contributed to the revisions of the manuscript. Q21

**Competing interests** The authors declare no competing interests. Q23

**Additional information**

**Supplementary information** The online version contains supplementary material available at https://doi.org/10.1038/s41586-025-08688-7.

**Correspondence and requests for materials** should be addressed to Thiago Gonçalves-Souza.

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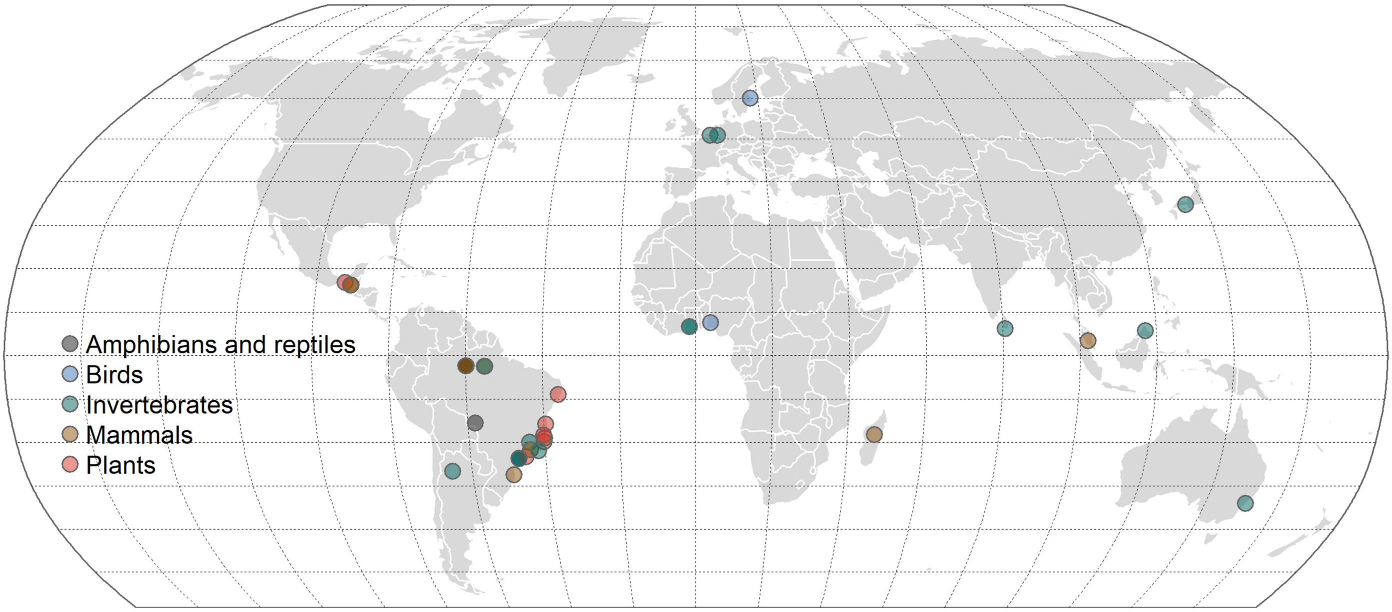
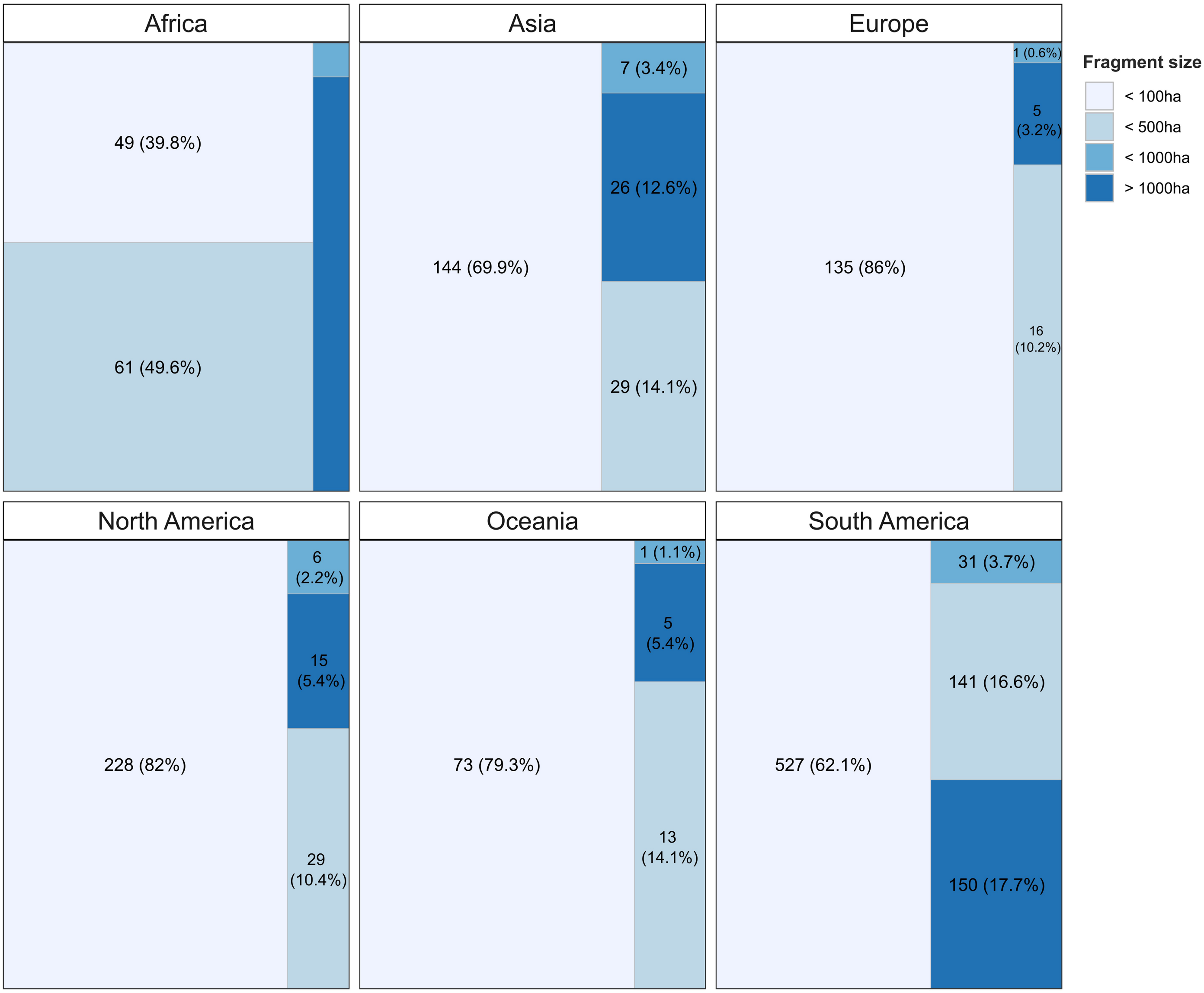
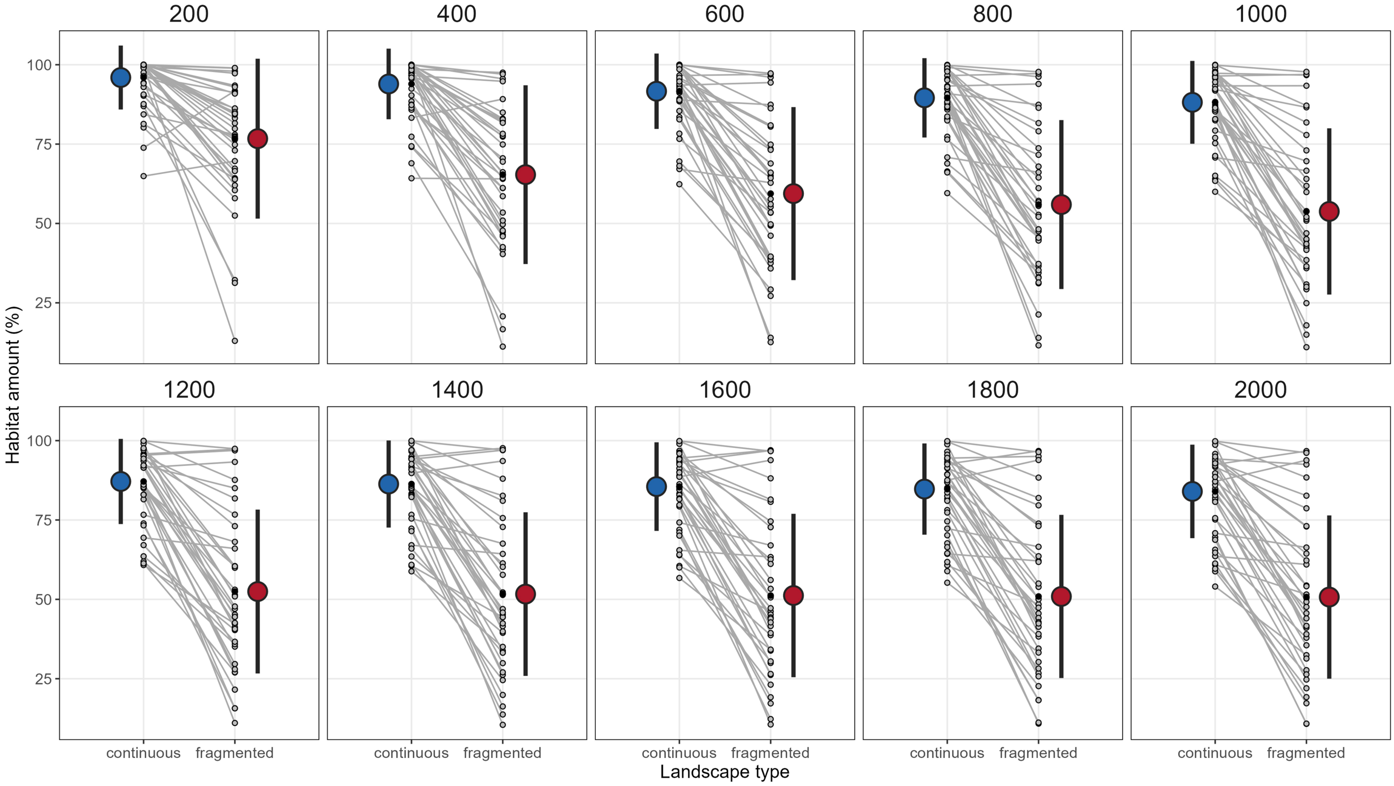


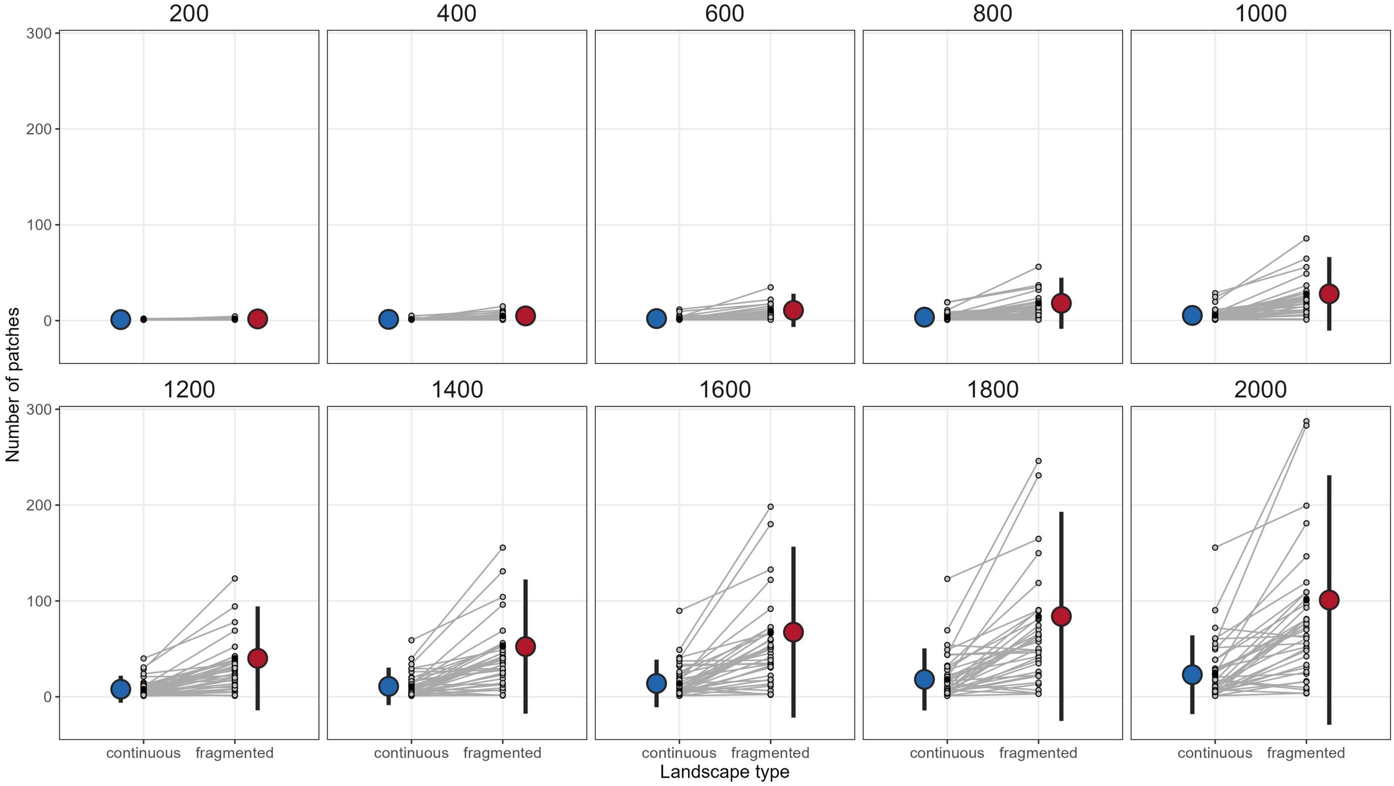
**Extended Data Fig. 1 | Study locations.** A global map displaying the locations of the 37 studies, as well as the taxonomic groups sampled in each. Made with Natural Earth. Free vector and raster map data from naturalearthdata.com.



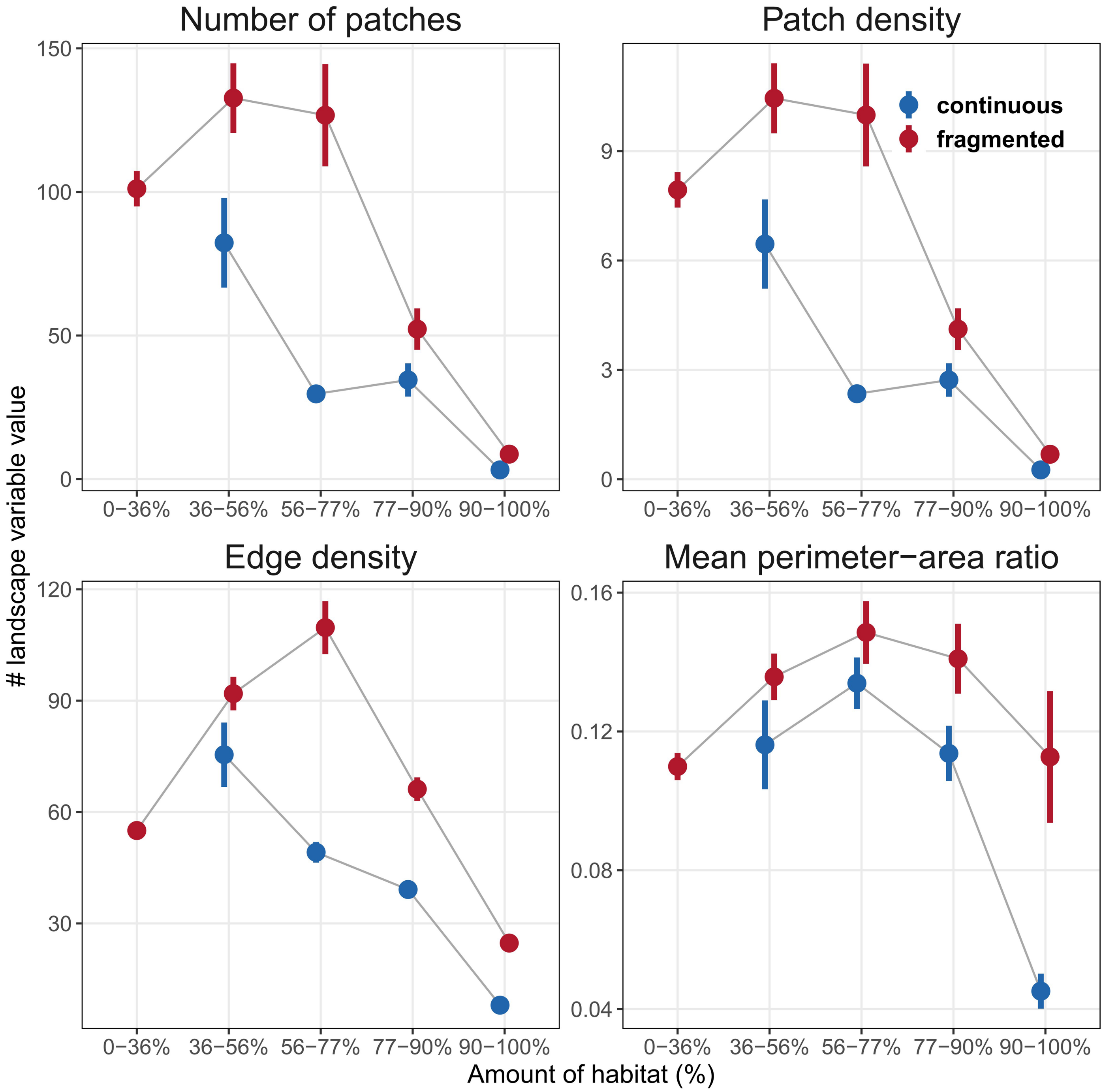
**Extended Data Fig. 2 | Fragment size classes.** Number (and percentage) of fragments or continuous forests in each fragment size class, which included fragments smaller than 100, 500 and 1,000 ha, as well as forest larger than 1,000 ha. The values were calculated using all 121 studies from the LandFrag dataset[51].



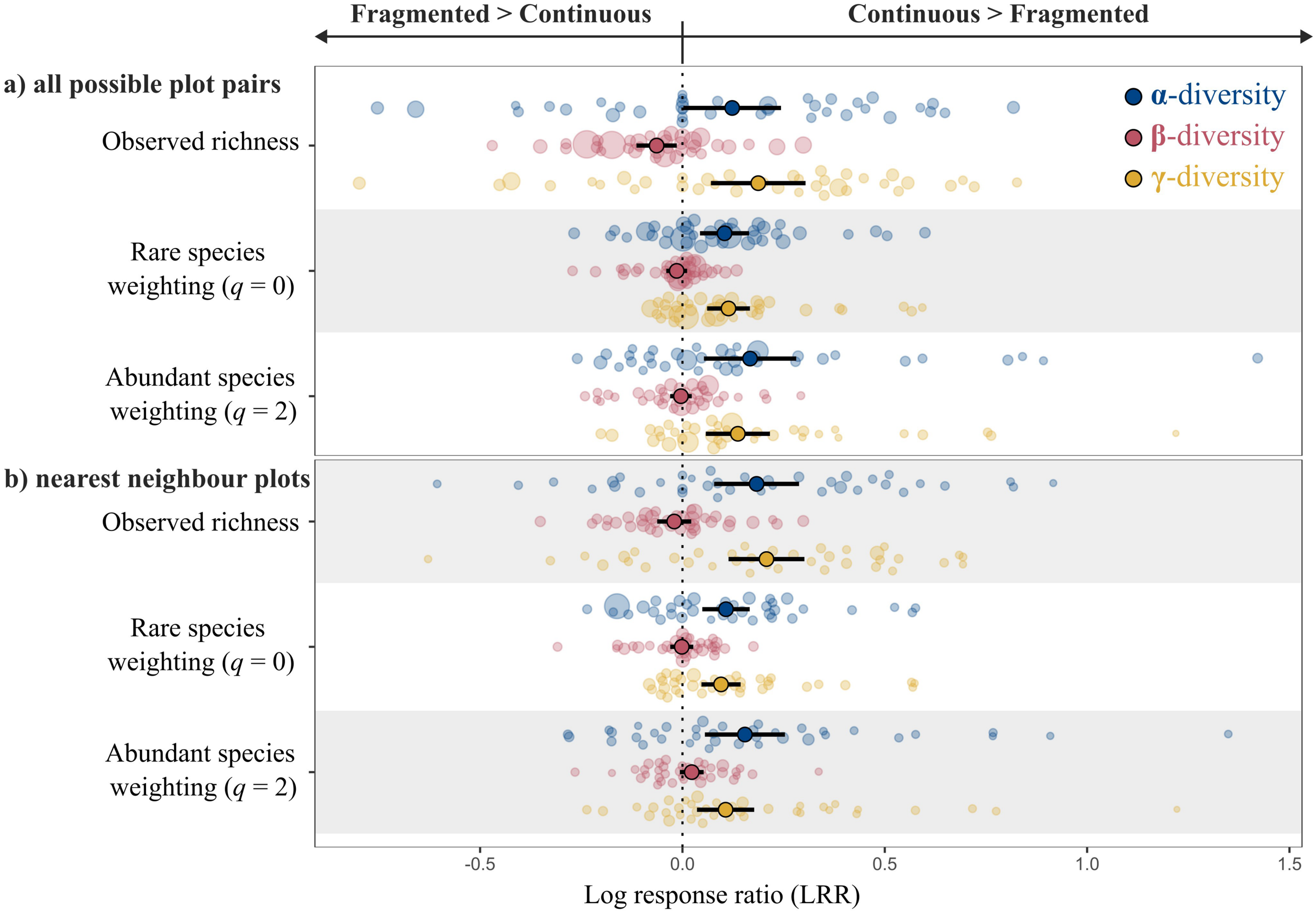
**Extended Data Fig. 3 | Habitat amounts in continuous and fragmented landscapes across all buffer sizes.** The buffer size ranged from a radius of 200 m to 2,000 m, in 200 m increments. Large circles represent the mean habitat amount in continuous (blue circles) and fragmented (red circles) landscapes across studies (n = 37). In all panels, each study is represented by a small grey circle, with lines connecting the landscape types, and error bars represent standard deviations.



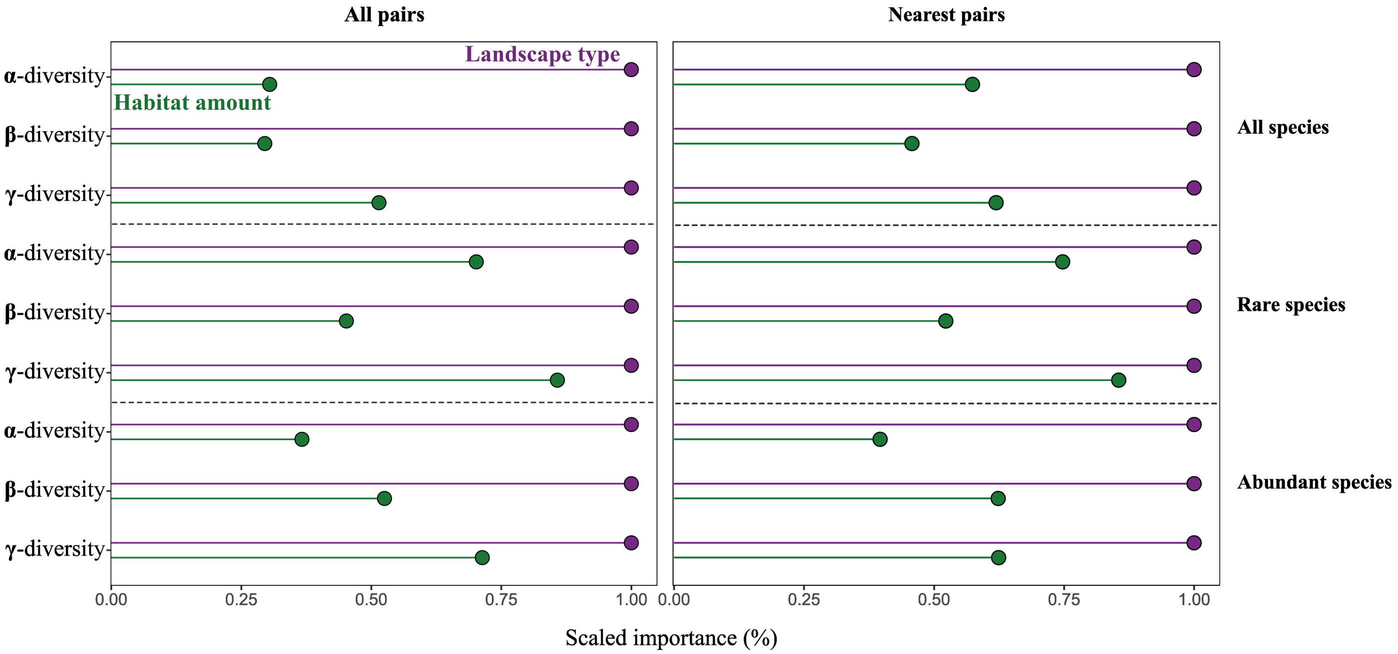
**Extended Data Fig. 4 | Number of patches in continuous and fragmented landscapes across all buffer sizes.** The buffer size ranged from a radius of 200 m to 2,000 m, in 200 m increments. Large circles represent the mean habitat amount in continuous (blue circles) and fragmented (red circles) landscapes across studies (n = 37). In all panels, each study is represented by a small grey circle, with lines connecting the landscape types, and error bars represent standard deviations.



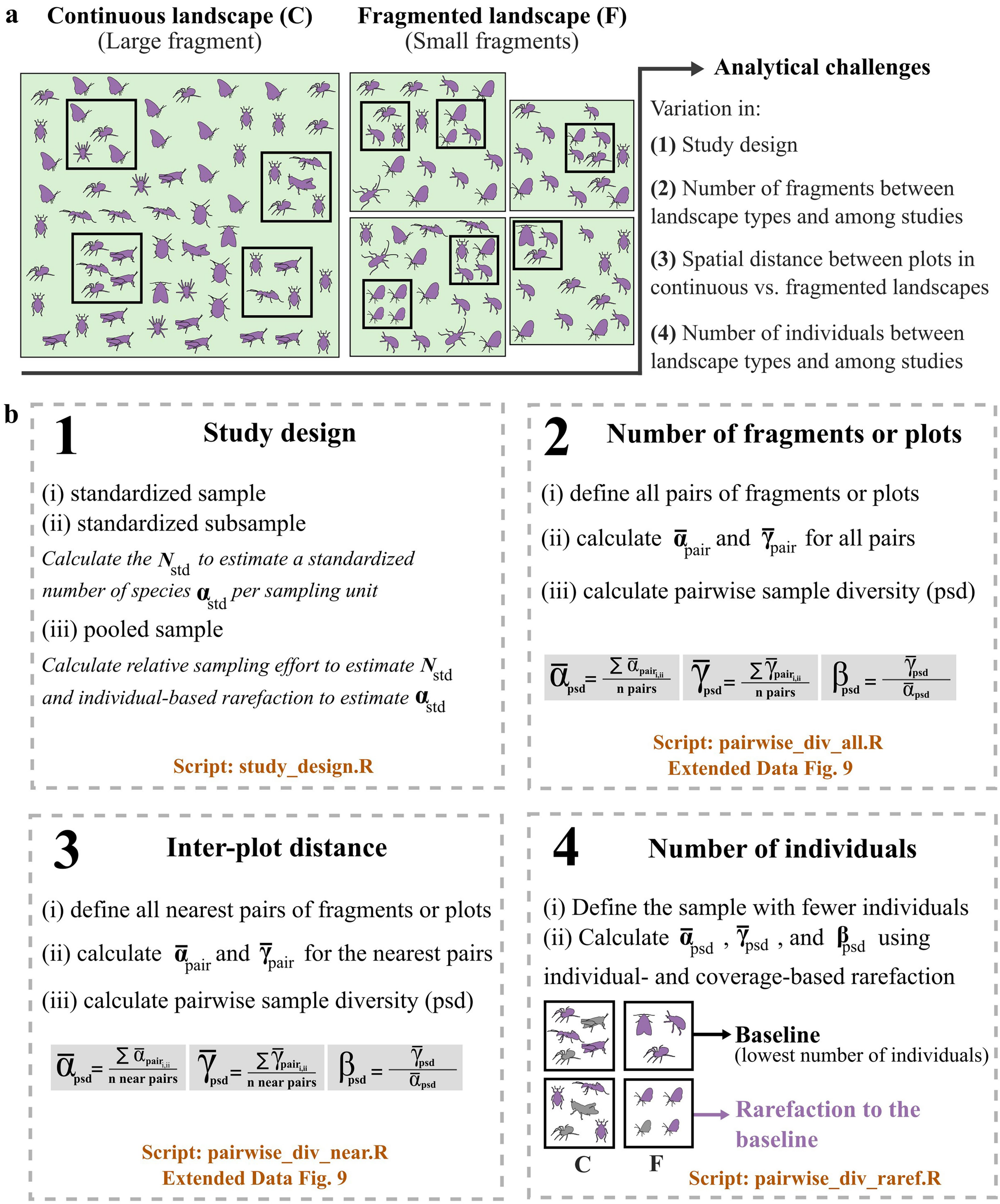
**Extended Data Fig. 5 | Variation in landscape variables related to fragmentation between continuous and fragmented landscapes across all studies.** Dots represent the average value (error bars ± 1 s.e.) of the landscape variable (buffer radius = 2,000 m) in a given habitat amount class (*n* = 37 studies).



**Extended Data Fig. 6 | Differences in α, β and γ diversity between fragmented and continuous landscapes using a meta-analytical approach.** This orchard plot shows the effect size (log-response ratio, LRR) of the overall difference between continuous and fragmented landscapes across studies (n = 37). The values of α, β and γ diversity were computed using (a) all possible plot pairs or (b) only the nearest plot pairs (controlling for distance decay effects) in both continuous and fragmented landscapes. We also calculated α, β and γ diversity using the observed species richness without controlling for commonness or sampling effort, and with individual-based rarefaction giving greater relative weight to rare species (rarefied species richness; *q* = 0) and individual-based rarefaction giving greater relative weight to abundant species (effective number of species given Simpson diversity; *q* = 2). Solid points represent the LRR comparing α, β and γ diversity between continuous and fragmented landscapes, and the error bars represent 95% confidence intervals. Positive effect sizes indicate that continuous landscapes have higher diversity than fragmented landscapes, while negative effect sizes would indicate that fragmented landscapes have higher diversity. Transparent points indicate effect sizes from individual sites, and their sizes are proportional to the precision (inverse of the square root of the variance) of the individual effect size estimates.

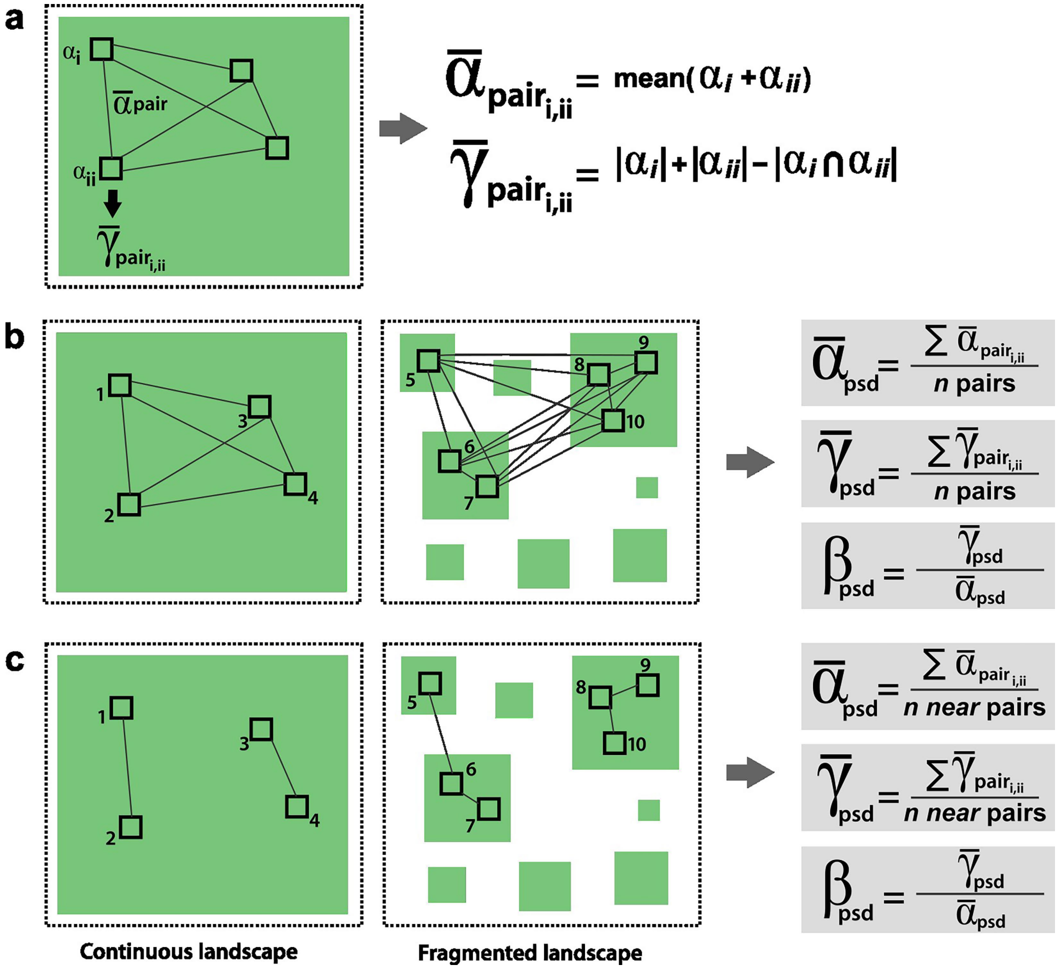


**Extended Data Fig. 7 | Individual contribution of landscape type and habitat amount to α, β and γ diversity.** As described in the main text, this analysis represents the scaled importance of predictor variables in GLMMs. The most important variable (that is, the one with the highest unbiased AICc weight value) in a given model receives a value of 1, and the relative contribution of the other variables is calculated based on this benchmark. We performed these analyses using all species, as well as using rarefaction analyses to give weight to rare (order $q = 0$) and abundant (order $q = 2$) species.

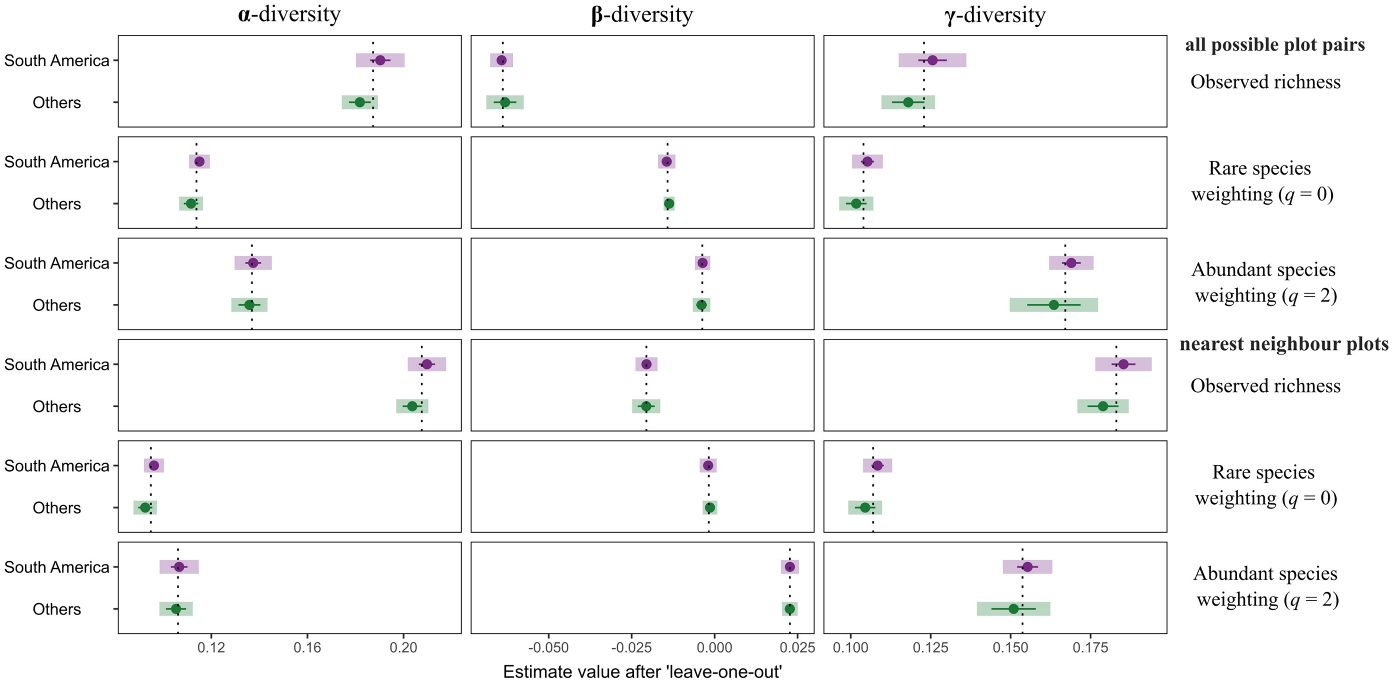


**Extended Data Fig. 8** | See next page for caption.

**Extended Data Fig. 8 | Illustration of the analytical pipeline used to standardize species diversity comparisons between continuous and fragmented landscapes. a**, The grey squares represent one large forest in a continuous landscape and four small fragments in a fragmented landscape. The small black squares represent a sample and illustrate how differences in size generally affect the number of samples when comparing landscape types. Furthermore, when comparing these landscape types, there are at least four analytical challenges (1–4) that affect our ability to estimate and compare α, β, and γ diversity. **b**, Analytical approach used to estimate diversity by (1) standardizing α diversity while accounting for differences in study design and sampling effort, (2) standardizing β and γ diversity by calculating pairwise sample diversity, (3) controlling for distance decay effects to accurately estimate α, β, and γ diversity, and (4) standardizing α, β, and γ diversity through consistent sampling effort adjustments across landscapes. Silhouettes from PhyloPic (http://phylopic.org/), as a courtesy of Andy Wilson, Birgit Lang, Lauren Sumner-Rooney, Mattia Menchetti, Dorota Paczesniak, Birgit Lang, Wouter Koch, Guillaume Dera, Graham Montgomery and Gareth Monger.



**Extended Data Fig. 9 | Method to calculate pairwise diversity for α, β and γ using a patch-landscape study design. a**, The average α diversity for each pair is calculated as the mean number of species in pair *i* and pair *ii*, while γ diversity is the pooled 'total' number of distinct species in a given pair (accounting for the overlap of shared species occurring in both pairs). This pair is selected using two approaches. **b**, All possible pairs in fragmented or continuous landscapes in each study. **c**, Only the nearest pairs to control for the effect of distance decay on β and γ diversity. The black squares represent a plot, numbered between 1 and 10. Therefore, a pair can consist of either two plots within the same forest or fragment, or two plots in different fragments.



**Extended Data Fig. 10 | Estimated mixed-effects meta-analysis coefficients using the 'leave-one-out' analysis to compare the effects of removing one study from South America versus other continents.** Error bars represent 95% confidence intervals, shaded areas represent standard deviations, and points indicate the average coefficient by continent groups (South America in purple vs. other continents in green). The vertical dashed lines represent the observed coefficient value for the main model (n = 37 studies). We estimated α, β and γ diversity using all species, as well as giving greater relative weight for rare ($q = 0$) or abundant ($q = 2$) species in two scenarios: all plot pairs and the nearest plot pairs.