The importance of diversity for ecosystem functioning increases in heterogeneous environments

Annemarie Wurz[1]* & Jörg Albrecht[2]*, Katrin Böhning-Gaese[2,3], Roland Brandl[4], Eike Lena Neuschulz[2], Jörg Bendix[5], Markus Fischer[6], Andreas Hemp[7], Jürgen Homeier[8], Ralf Kiese[9], Yakov Kuzyakov[10], Christoph Leuschner[11], Marcell K. Peters[12], Stefan Scheu[13,14], Ingolf Steffan-Dewenter[12], Andre Velescu[15], Wolfgang Wilcke[15], Matthias Schleuning[2]** & Nina Farwig[1]**

*shared first authorship **shared last authorship

[1]Department of Biology, Conservation Ecology, University of Marburg, Marburg, Germany
[2]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany
[3]Department of Biological Sciences, Johann Wolfgang Goethe-University Frankfurt, Biologicum, Frankfurt am Main, Germany
[4]Department of Ecology, Animal Ecology, University of Marburg, Marburg, Germany
[5]Department of Geography, Laboratory for Climatology and Remote Sensing, University of Marburg, Marburg, Germany
[6]Institute of Plant Sciences, University of Bern, Bern, Switzerland
[7]Department of Plant Systematics, University of Bayreuth, Bayreuth, Germany
[8]Resource Management, University of Applied Sciences and Arts (HAWK), Göttingen, Germany
[9]Karlsruhe Institute of Technology, Institute for Meteorology and Climate Research (IMK-IFU), Garmisch-Partenkirchen, Bayern, DE
[10]Department of Soil Science of Temperate Ecosystems, and Department of Agricultural Soil Science, University of Göttingen, Göttingen, Germany
[11]Plant Ecology and Ecosystems Research, University of Göttingen, Göttingen, Germany.
[12]Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, Würzburg, Germany
[13]J.-F. Blumenbach Institute of Zoology and Anthropology, University of Göttingen, Göttingen, Germany
[14]Centre of Biodiversity and Sustainable Land Use, University of Göttingen, Göttingen, Germany
[15]Institute of Geography and Geoecology (IFGG), Karlsruhe Institute of Technology (KIT), Reinhard-Baumeister-Platz 1, 76131 Karlsruhe, Germany

Corresponding authors: Annemarie Wurz wurz@staff.uni-marburg.de and Jörg Albrecht joerg.albrecht@senckenberg.de

Abstract and keywords

Aim

Significant progress has been made in understanding the links between biodiversity and ecosystem functioning in both experimental and real-world ecosystems. Yet, we have limited understanding to which extent biodiversity affects ecosystem functioning in natural heterogeneous environments and whether changes in ecosystem functions are related to changes in species richness and/or turnover. Here we (1) quantify the contribution of diversity to variation in ecosystem functioning (i.e., the diversity effect) in heterogeneous environments and (2) test whether spatial variation in species richness and/or turnover between communities mediate effects of environmental heterogeneity on the diversity effect.

Location

Two tropical elevational gradients: Andes (Ecuador) and Mt. Kilimanjaro (Tanzania).

Time period

Current.

Taxa studied

Multiple: plants, oribatid mites, springtails, ants and birds.

Methods

We expand an analytical framework based on the Price equation to quantify the relative contribution of species richness or turnover to variation in ecosystem functioning within and across ecosystem types. We applied this framework using data on seven ecosystem functions collected in six ecosystem types on two tropical elevational gradients.

Results

We found a consistent increase in the diversity effect on ecosystem functioning with increasing environmental heterogeneity. Both species richness and turnover contributed similarly to the diversity effect. The increase in the diversity effect with environmental heterogeneity was solely based on the variation in species richness. The effect of species turnover was unrelated to environmental heterogeneity.

Main Conclusions

Our proposed framework enables the quantification of BEF relationships at large spatial scales and across various ecosystem types. It expands on previous studies by allowing comparisons among naturally assembled communities along environmental gradients. By applying our framework to two tropical systems, we show that changes in species richness and turnover contribute similarly to variations in ecosystem functioning across both elevational gradients. However, species richness is particularly important in mediating the effects of environmental heterogeneity on ecosystem functioning.

Keywords

Biodiversity, environmental heterogeneity, ecosystem functioning, price equation, species richness, species turnover, tropical mountains

Introduction

Global change is causing a substantial modification and reorganization of biodiversity (Blowes et al., 2019; Newbold et al., 2019). Understanding the consequences of biodiversity change for ecosystem functioning is important for human well-being (e.g. Díaz et al., 2006). Numerous experiments have investigated the effect of species richness on ecosystem functioning (Biodiversity-Ecosystem Functioning [BEF] experiments hereafter; e.g. Hooper et al., 2012; Weisser et al.,

2017) and have shown that biodiversity and ecosystem functioning are usually positively related (e.g. Brose & Hillebrand, 2016). In these experiments, the effect of species loss on ecosystem functioning can be as strong as the direct effects of environmental factors on ecosystem functioning (Hooper et al., 2012). In natural systems, however, the effects of biodiversity on ecosystem functioning are difficult to quantify due to the heterogeneity in environmental conditions and community composition and, hence, may be more variable than in small-scale experiments (van der Plas, 2019). One reason for this variability is that community composition strongly affects ecosystem functioning, i.e., a large number of rare species in natural communities might result in negative relationships between biodiversity and ecosystem functioning (Dee et al., 2023). Moreover, the reorganization of communities through time could reduce ecosystem functioning even if species richness was unchanged (Blowes et al., 2019). Therefore, it remains debated how the experimental findings about biodiversity-ecosystem functioning relationships can be transferred to natural ecosystems at large spatial scales (Dee et al., 2023; van der Plas, 2019).

In natural ecosystems, environmental heterogeneity, such as spatial variation in climate and soil conditions, affects the relationship between biodiversity and ecosystem functioning and, thereby also the contribution of diversity to ecosystem functioning (Gonzalez et al., 2020; Lemanski et al., 2022; Winfree et al., 2018). The contributions of diversity to variation in ecosystem functioning between communities could be driven by two key processes: (i) variation in species richness and (ii) turnover in species identities among communities (Gonzalez et al., 2020; Huber et al., 2020). First, environmental heterogeneity can increase the variation in species richness among communities (Grace et al., 2016; Harpole et al., 2016). Second, environmental heterogeneity can increase species turnover among communities because species differ in their habitat requirements so that different species occur in different environments (Gonzalez et al., 2020). Depending on the prevailing process, variation in species richness, species turnover or both could drive the contribution of diversity to variation in ecosystem functioning (Albrecht et al., 2021). To isolate the contributions of variation in species richness and turnover to the diversity effect on ecosystem functioning, new analytical frameworks are required that are flexible enough to analyse variation in biodiversity-ecosystem functioning relationships at large spatial scales.

Here we expand a recently developed analytical framework to analyze BEF relationships in naturally assembled communities along continuous environmental gradients (Fig. 1; also see Albrecht et al., 2021). The framework builds on the assumption that variation in ecosystem functioning among communities can result from three proximate processes: (1) variation in species richness, (2) species turnover between communities, or (3) a change in the functional contributions of species that are shared between communities (for example, due to variation in abundance or individual performance; Albrecht et al., 2021). The framework combines a variant of the Price equation from evolutionary biology with the concept of β-diversity to quantify the relative contributions of these three mechanisms to variation in ecosystem functioning (Albrecht et al., 2021). We chose the Price equation over other methods because it decomposes changes in ecosystem function into components that reflect different ecological processes (Bannar-Martin et al., 2018; Fox, 2006; Fox & Kerr, 2012b). It effectively separates the effects of species richness and species composition, providing insights into how species richness and turnover influence ecosystem functioning. The applied variant of the Price function allows to analyse BEF relationships within and across ecosystem types by pairwise comparisons of communities (Fig. 1). The framework allows to quantify the contribution of diversity to variation in ecosystem functioning along continuous gradients of environmental heterogeneity. By applying the framework to real-world data, it is possible to quantify how variation in species richness and/or species turnover contribute to the diversity effect in natural environments (Fig. 1).

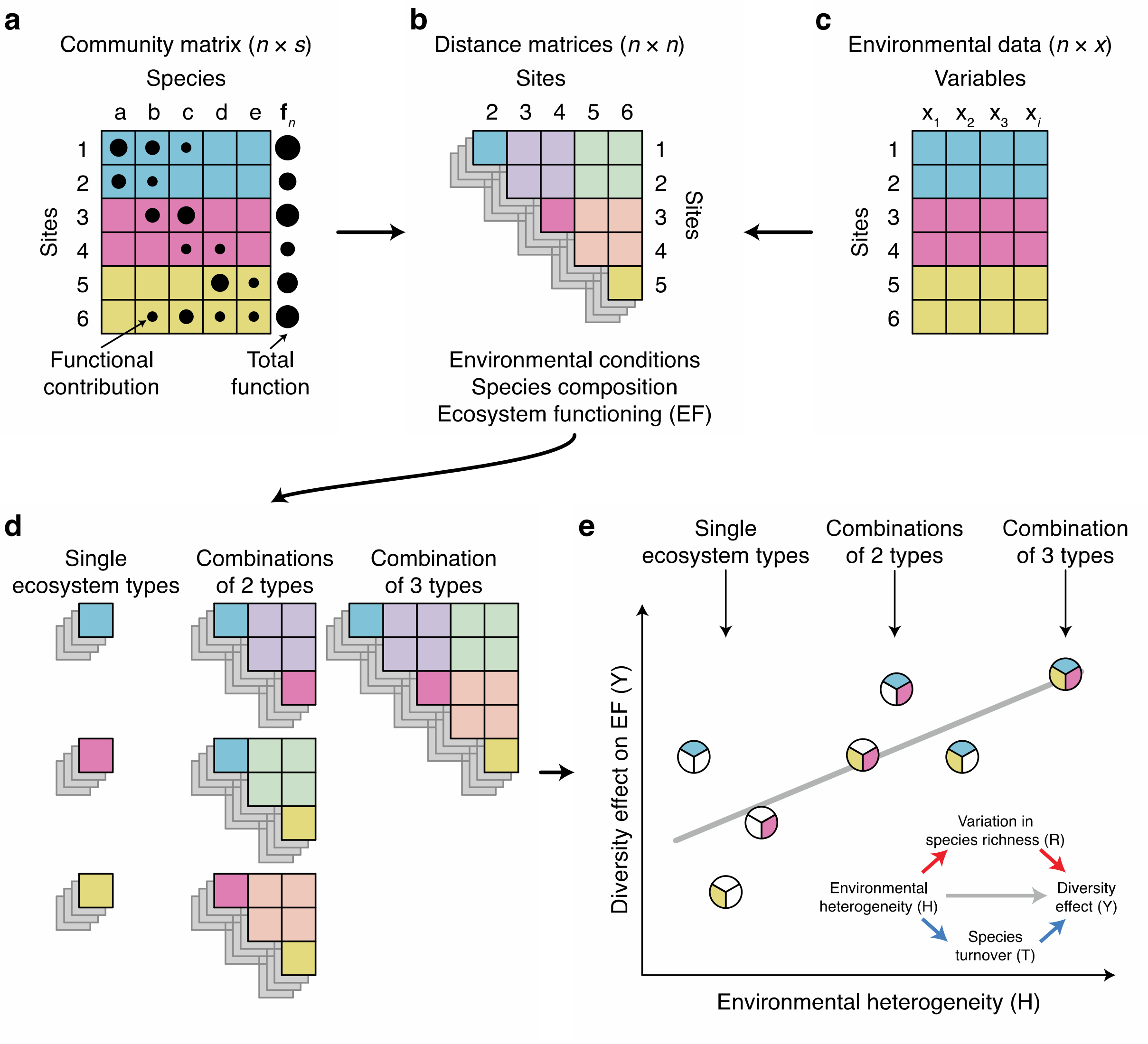

Figure 1. The proposed analytical framework to upscale the effect of diversity on ecosystem functioning across heterogeneous environments. (a) A community matrix showing the contribution (filled circles) of each species to ecosystem functioning at six sites belonging to three different ecosystem types (*akin* to increasing environmental heterogeneity; shading of cells in blue, red and yellow). The size of the filled circles corresponds to the magnitude of the functional contribution.

The total function of each community (f_n) is given by the sum of the species-specific functional contributions. (b) Distance matrices in which cells represent the pair-wise comparisons of sites of the same or different ecosystem types in terms of (i) variation in species richness and (ii) species turnover, as well as differences in (iii) ecosystem functioning and (iv) environmental variables. Colors correspond to pair-wise comparisons within the same (blue, red, and yellow) or between the ecosystem types (purple, green, and orange). (c) Site-specific environmental data that feed into pair-wise comparisons. (d) Pair-wise comparisons of communities based on combinations of one to three ecosystem types allow to compare the relative contribution of diversity to variation in ecosystem functioning (i.e., the 'diversity effect') between communities within and across multiple ecosystem types. (e) Hypothesized relationship of environmental heterogeneity with the diversity effect on ecosystem functioning (EF) based on the combination of one to three ecosystem types (number of possible combinations indicated by circles filled with different colors). The path diagram in (e) depicts the assumed causal relationships between environmental heterogeneity (H), variation in species richness (R), species turnover (T) and the diversity effect (Y) which can be quantified with the proposed framework.

We apply this framework to ecosystem functions of plants and animals, including biomass stocks of trees, birds, ants, and soil arthropods, as well as seed dispersal by birds, resource use by ants, and litter decomposition by soil arthropods. We study the relation between the diversity and functions of these taxa across six ecosystem types that cover a broad gradient of environmental conditions (e.g., climate, soil conditions, natural and disturbed ecosystems) in two tropical mountain regions: the Ecuadorian Andes in south-eastern Ecuador and Mt. Kilimanjaro in Tanzania. Both mountain regions have distinct biogeographic histories and therefore also distinct species pools. They are characterized by high biodiversity as well as topographic and climatic complexity (Rahbek et al., 2019), being ideal systems for quantifying the contribution of diversity to ecosystem functioning in heterogeneous environments. We use the framework to test two main hypotheses in the two mountain regions. (i) The diversity effect on ecosystem functioning increases with increasing environmental heterogeneity (Barnes et al. 2016; Martinez-Almoyna et al. 2019). (ii) The increase in the diversity effect with environmental heterogeneity is driven by differences in species richness rather than by species turnover (Albrecht et al., 2021).

Material and methods

Quantifying the contribution of diversity to ecosystem functioning. The framework is generally applicable to any ecosystem function that is determined by the summed functional contributions of individual species. It is based on a community matrix **F** ($n \times s$), which summarizes the contribution of s species to a given ecosystem function in n study sites (which we refer to as communities; Albrecht et al., 2021). Each element f_{ij} of matrix **F** represents the contribution of species j to a given ecosystem function at study site i. Using matrix **F**, we constructed three binary matrices **P**, **Q**, and **O**. Matrix **P** is a binary species incidence matrix (with the same dimensions as F, in which $p_{ij} = 1$ if $f_{ij} > 0$ and $p_{ij} = 0$ otherwise). Further, matrix **Q** is the complement of matrix **P** ($\mathbf{Q} = 1 - \mathbf{P}$), so that $q_{ij} = 1$ if $f_{ij} = 0$ and $q_{ij} = 0$ otherwise. And finally, matrix **O** is given by the sum of matrices **P** and **Q**, so that all elements $o_{ij} = 1$. The total difference in the magnitude of a given ecosystem function between two communities i and j is given by the element Δf_{ij} of the $n \times n$ square matrix $\Delta\mathbf{F} = \mathbf{FO}^{\mathrm{T}} - \mathbf{OF}^{\mathrm{T}}$. The difference in the magnitude of an ecosystem function between two communities i and j caused by changes in the functional contributions of shared species is given by the element Δs_{ij} of the $n \times n$ square matrix $\Delta\mathbf{S} = \mathbf{FP}^{\mathrm{T}} - \mathbf{PF}^{\mathrm{T}}$. Lastly, the difference in the magnitude of a given ecosystem function between two communities i and j caused by differences in species richness and species turnover between communities is represented by the element Δd_{ij} of the $n \times n$ square matrix $\Delta\mathbf{D} = \mathbf{FQ}^{\mathrm{T}} - \mathbf{QF}^{\mathrm{T}}$. It follows that:

$$\Delta f_{ij} = \Delta d_{ij} + \Delta s_{ij} \quad (1)$$

Equation (1) comprises three components that possess the dimension of the corresponding ecosystem function and an expected value of zero if there is no overall difference in this function between communities *i* and *j* ($\Delta f_{ij} = 0$), no difference in function because of differences in species richness and species turnover ($\Delta d_{ij} = 0$), or no difference in function because of differences in the functional contributions of shared species ($\Delta s_{ij} = 0$). The components can be positive or negative, and the diversity and shared species components may cancel each other out, resulting in a net difference in the function of zero. Note that the formula presented in equation (1) corresponds to the community-assembly-decomposition of the Price equation by Bannar-Martin et al. (2018). However, the formulation described here overcomes an important limitation of previous frameworks (Bannar-Martin et al., 2018; Fox & Kerr, 2012a), as it can be used for any pair of communities, regardless of whether they have species in common.

Using equation (1), we calculated the relative contribution of the diversity of the focal taxa to variation in their ecosystem functions between communities, which we refer to as the diversity effect (Y).

$$Y = \frac{\sum_{i<j}^{n} |\Delta d_{ij}|}{\left(\sum_{i<j}^{n} |\Delta d_{ij}| + \sum_{i<j}^{n} |\Delta s_{ij}|\right)} \qquad (2)$$

Where the absolute values of Δd_{ij} and Δs_{ij} are denoted as $|\Delta d_{ij}|$ and $|\Delta s_{ij}|$, respectively. Absolute values are used because Δd_{ij} and Δs_{ij} can either be positive or negative, thus computing the mean of these values would mask the total contribution of both factors. The diversity effect is a dimensionless measure that ranges from 0 to 1. The diversity effect equals 0 if all differences in ecosystem functioning between communities result from differences in the functional contributions of shared species, which can be attributed to differences in abundance or individual performance. Conversely, the diversity effect equals 1 if all differences in ecosystem functioning result from the combined effects of differences in species richness and turnover between communities. For worked example scenarios of how changes in species richness, species turnover, or the functional contribution of shared species are related to the diversity effect see Appendix Fig. S1.1 in Supporting Information.

Quantifying the variation in species richness and turnover. We used the Jaccard index to partition the variation in species composition (β) into variation resulting from differences in species richness (R) and species turnover (T) between n communities (Albrecht et al., 2021). The species richness and turnover components form an additive partition of the total variation in species composition, meaning that $\beta = R + T$ (Legendre, 2014). To estimate the total variation in species composition and its two components, we calculated the number of shared species, unique species in community i, and unique species in community j, using the species incidence matrix $\mathbf{P}$ and its complement $\mathbf{Q}$. The number of shared species between communities i and j is represented by element a_{ij} of the $n \times n$ matrix $\mathbf{A} = \mathbf{P}\mathbf{P}^{\mathrm{T}}$, the number of species unique to community i by element b_{ij} of the $n \times n$ matrix $\mathbf{B} = \mathbf{P}\mathbf{Q}^{\mathrm{T}}$, and the number of species unique to community j by element c_{ij} of the $n \times n$ matrix $\mathbf{C} = \mathbf{Q}\mathbf{P}^{\mathrm{T}}$. Using these matrices, we can express the total variation in species composition (β), the richness component (R), and the turnover component (T) as:

$$\beta = \frac{2}{n(n-1)} \sum_{i<j}^{n} \frac{b_{ij}+c_{ij}}{a_{ij}+b_{ij}+c_{ij}} \qquad (3)$$

$$R = \frac{2}{n(n-1)} \sum_{i<j}^{n} \frac{|b_{ij}-c_{ij}|}{a_{ij}+b_{ij}+c_{ij}} \qquad (4)$$

$$T = \frac{2}{n(n-1)} \sum_{i<j}^{n} \frac{2min(b_{ij},c_{ij})}{a_{ij}+b_{ij}+c_{ij}} \quad (5)$$

Quantifying environmental heterogeneity. We used the Gower distance to determine the environmental distance *h* between sites based on a set of environmental variables. The Gower distance between two sites *i* and *j* equals the mean difference in environmental variables across all environmental variables after standardizing the environmental variables by their ranges:

$$h_{ij} = \frac{1}{n} \sum_{k=1}^{n} \frac{|x_{ik} - x_{jk}|}{(max\, x_k - min\, x_k)} \quad (6)$$

In equation (6), *n* is the number of environmental variables, x_{ik} and x_{jk} are the values of variable *k* on study sites *i* and *j.* The Gower distance is preferred over the Euclidean distance as it is less sensitive to extreme values and facilitates the inclusion of categorical measures. Moreover, the range standardization ensures that each environmental variable contributes equally to the distance metric, and the maximum value of the distance function is 1. As some study sites had missing data for some environmental variables, we calculated the pairwise distances by using a pairwise deletion of missing observations. We defined environmental heterogeneity (*H*) as the mean environmental distance between *n* combinations of study sites:

$$H = \frac{2}{n(n-1)} \sum_{i<j}^{n} h_{ij} \quad (7)$$

Quantifying how environmental heterogeneity modulates the effect of diversity on ecosystem functioning. To quantify the direct effect of environmental heterogeneity on the diversity effect as well as the indirect effects that are mediated by variation in species richness and species turnover within and across ecosystem types, we segmented the distance matrices for Y, R, T and H into submatrices that contained comparisons within single and across multiple ecosystem types (Fig. 1d). Then, we averaged these submatrices to obtain estimates for Y, R, T and H for comparisons between sites based on different numbers of ecosystem types (Fig. 1e).

Case study.

To apply the framework to empirical data, we used data from two tropical mountain regions located in the Ecuadorian Andes, south-eastern Ecuador, and on Mt. Kilimanjaro, Tanzania. In both mountain regions, we investigated an elevational gradient of approximately 1,000 to 3,000 m a.s.l. including near-natural (thereafter called undisturbed) and human-modified (thereafter called disturbed) forest ecosystems. On both studied mountain systems, we assessed ecosystem functions and species richness on a common pool of sites, but not all functions could be measured on every study site. In the Ecuadorian Andes, the number of study sites for each function and taxon diversity ranged between 15 and 67 (median = 18 study sites; see Appendix Table S1.1 in Supporting Information for more details on the numbers of study sites per function). The study sites covered the following ecosystem types: undisturbed and disturbed premontane forest (960–1,268 m a.s.l.), undisturbed and disturbed lower montane forest (1,850–2,450 m a.s.l.), undisturbed and disturbed upper montane forest (2,679–2,931 m a.s.l.). On Mt. Kilimanjaro, the number of study sites for each function ranged between 12 and 30 (median = 29 study sites). The study sites covered the following ecosystem types: undisturbed and disturbed lower montane forest (1,171–2,097 m a.s.l.), undisturbed and disturbed *Ocotea* forest (2,150–2,741 m a.s.l.), undisturbed and disturbed *Podocarpus* forest (2,753–3,009 m a.s.l.; see Table S1.2 for more details on the disturbance types).

Environmental variables. We characterized environmental heterogeneity by combining soil, mean annual air temperature, and annual precipitation data (Appendix S1, Soil and Climate variables). Mean annual temperature was highly correlated with elevation on both mountains, thus elevation was not included in the calculation of environmental heterogeneity. To characterize soils, we used topsoil organic carbon content and C/N and N/P ratios (Appendix S1 Soil variables).

Ecosystem functions. The framework requires information about the contribution of each species to ecosystem functioning in each community. We focussed on seven ecosystem functions including aboveground biomass stocks of woody plants, biomass stocks of birds, ants, oribatid mites (Ecuadorian Andes) and springtails (Mt. Kilimanjaro), as well as process rates for seed dispersal by birds, resource use by ants, and litter decomposition by oribatid mites (Ecuadorian Andes) and springtails (Mt. Kilimanjaro; Appendix S1 Methods, Ecosystem functions). We used standing biomass stock as a proxy for ecosystem functioning because it represents the accumulated result of various ecosystem processes (e.g., growth, energy storage, resource acquisition) and is a widely used indicator of ecosystem health and productivity (Loreau et al., 2021; O'Connor et al., 2017; Tilman, 1997). For six of the seven functions, we had direct estimates of species-specific functional contributions in each community. For litter decomposition, direct estimates of species-specific functional contributions were not available. Therefore, we used site-level data on decomposition rates and allocated portions of the total ecosystem function in a given community proportional to the relative abundances or biomass of the species in that community (Garnier et al., 2004; Winfree et al., 2015). Detailed sampling protocols for each ecosystem function are provided in Appendix S1 (Methods, Ecosystem functions).

Statistical analysis

We applied the framework to data from both mountain regions by calculating pair-wise distance matrices of environmental variables, species composition, and ecosystem functioning for each function across ecosystem types (see Figure 1). We aggregated these distance matrices for combinations of one to six ecosystem types separately for each of the seven functions and each mountain region and used the aggregated matrices to obtain estimates for the relative contribution of diversity to variation in ecosystem functioning (i.e., the diversity effect), variation in species richness, species turnover and environmental heterogeneity within and across multiple ecosystem types. For the analysis, we also recorded the identity of the ecosystem types that were included in the underlying pair-wise comparisons between sites.

To test our first hypothesis, we fitted a multiple-membership mixed-effects model (MMMEMs) (Park & Beretvas, 2020) to the data from both mountain regions to analyze the diversity effect within and across multiple ecosystem types (Table S1.3). In this model, we treated the diversity effect as the response variable and environmental heterogeneity as the predictor variable. Moreover, we included correlated random factors for intercepts and slopes associated with the identity of the ecosystem functions into the model to account for variation in the relationship between the diversity effect and environmental heterogeneity between different types of ecosystem functions. In addition, we included a multiple-membership random-effects structure associated with the identity of ecosystem types in the model to account for the non-independence of pair-wise comparisons involving the same ecosystem types (Park & Beretvas, 2020). The multiple membership structure was based on the identity of the ecosystem types that were included in the pair-wise comparisons between study sites. In the initial model, we also included region identity (Ecuadorian Andes and Mt. Kilimanjaro) as a fixed factor and its interaction with environmental heterogeneity. A comparison of this model to a model without the interaction term based on the Bayesian Information Criterion (BIC) suggested that the relationship between the diversity effect and environmental heterogeneity did not differ between the two regions (Table S1.4). Therefore, we report the results of the model without the interaction term in the main text.

To test our second hypothesis, we fitted a structural equation model (SEM) based on MMMEMs to assess the direct effect of environmental heterogeneity on the diversity effect, as well as the indirect effects that were mediated via variation in species richness and species turnover (Fig. 1e). To do so, we constructed three MMMEMs (sub-models hereafter) that described the implied causal structure of the SEM (Fig. 1e; Table S1.5). In the first sub-model, we treated variation in species richness as the response variable and environmental heterogeneity as the predictor variable. In the second sub-model, we treated species turnover as the response variable and environmental heterogeneity as the predictor variable. In the third sub-model, we treated the diversity effect as the response variable and environmental heterogeneity, variation in species richness, and species turnover as predictor variables. In all of these models, we included correlated random factors for intercepts and slopes associated with the identity of the ecosystem functions to account for variation in the relationships between the response and predictor variables between different types of ecosystem functions. In addition, we included a multiple-membership random-effects structure in the model as described above. We included region identity and its interaction with the other explanatory variables in the initial model to test for differences in the relationships between regions (Table S1.6). A comparison of this model to a model without the interaction term based on BIC indicated that the relationships did not differ between the two regions (Table S1.6). Therefore, we report the results of the SEM without the interaction terms in the main text.

We also assessed the raw relationships between species richness and ecosystem functioning across ecosystem types (Fig. S1.2). To do so, we fitted a single linear mixed effects model (MEM) to the data from both mountain regions to analyze the relationship between species richness and ecosystem functioning (Table S1.7). In this model, we treated the magnitude of ecosystem functioning ($\log_{10}$-transformed) as the response variable and species richness ($\log_{10}$-transformed) as the predictor variable. Data were log-transformed because the relationships were non-linear and the data was quite skewed towards small values. Moreover, we included correlated random factors for intercepts and slopes associated with the identity of the ecosystem functions into the model to account for variation in the relationship between species richness and ecosystem functioning between functions. As before, we compared models with and without an interaction term between region and species richness based on BIC (Table S1.8). As the relationships did not differ between the two regions (Table S1. 8), we report the results of the model without the interaction terms in the main text. As before, we also included region identity (Ecuadorian Andes and Mt. Kilimanjaro) as a fixed factor and its interaction with species richness in the initial model. A comparison of this model to a model without the interaction term based on BIC suggested that the relationship between species richness and ecosystem functioning did not differ between regions (Table S1.8).

All analyses were conducted in R language (R Core Team, 2023). The MMMEMs and the MEM were implemented in the *lme4* package (Bates et al., 2015). We used customized code for fitting the MMMEMs in *lme4*. The models were checked for convergence and singularity using the *performance* package (Lüdecke et al., 2021). All models converged and no singularity was detected. Model selection was done using the *MuMIn* package (Barton, 2023).

Results

On both mountains, the magnitude of ecosystem functioning generally increased with increasing species richness (slope: 1.1 [0.46—1.7, 95% CI], $z = 3.6$, $P < 0.001$; $R^2_m = 0.25$; Fig. S1.2 and Table S1.5). The positive relationship between species richness and ecosystem functioning was found for all ecosystem functions, except for the resource use of ants in the Ecuadorian Andes (Fig. S1.2).

In line with our first hypothesis, the diversity effect increased with increasing environmental heterogeneity in both mountain regions (Fig. 2), with an average increase of 1.1% in the diversity effect for a 1% increase in environmental heterogeneity (0.57%—1.6%, 95% CI, $z = 4.4$, $P < 0.001$; Table S1.5). The contribution of diversity to variation in ecosystem functioning was largest for soil arthropod biomass and woody plant biomass in the Ecuadorian Andes, and for ant biomass and resource use on Mt. Kilimanjaro (Fig. 2). The strongest increases in the diversity effect with increasing environmental heterogeneity were observed for seed dispersal by birds and ant biomass in the Ecuadorian Andes and for woody plant biomass and litter decomposition on Mt. Kilimanjaro (Fig. 2).

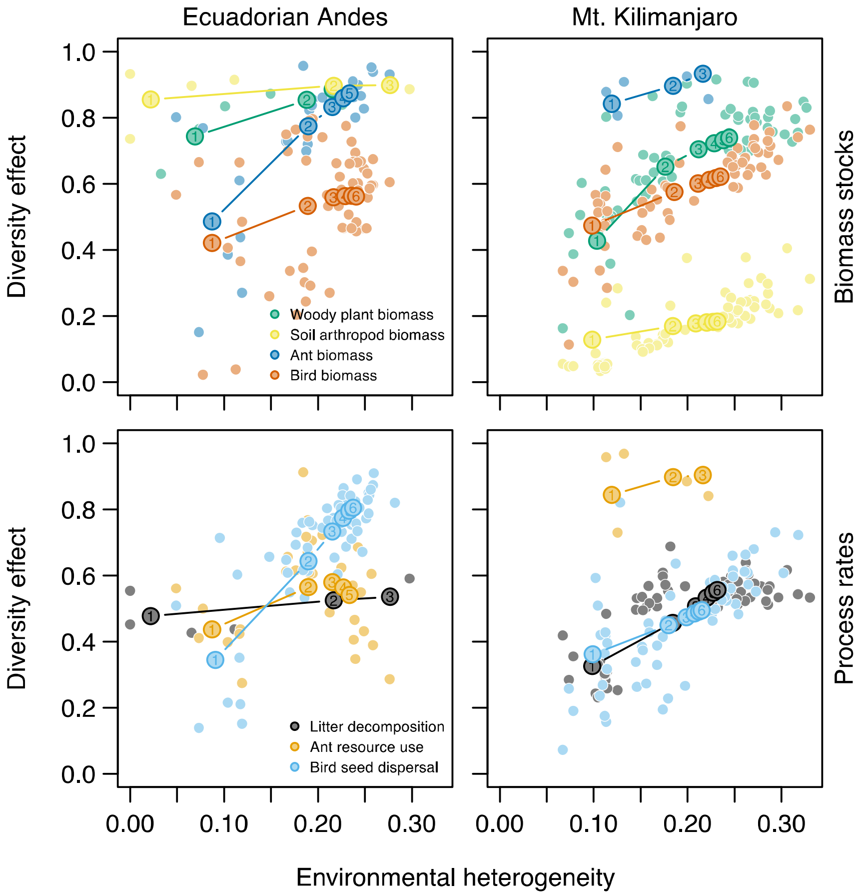

Figure 2. Relationship between environmental heterogeneity and the contribution of diversity to variation in ecosystem functioning. For two mountain regions, the relationship between the diversity effect (i.e., the relative contribution of diversity to variation in each ecosystem functioning) and environmental heterogeneity is shown for seven ecosystem functions related to biomass stocks of woody plants, soil arthropods, ants, and birds, as well as process rates related to litter decomposition by soil arthropods, resource use by ants and seed dispersal by frugivorous birds. Larger circles connected by lines represent the trend in the mean diversity effect as environmental heterogeneity increases across the range of combined ecosystem types for each ecosystem function (number of combined ecosystem types indicated within circles). The smaller light-coloured dots in the background depict the unaggregated raw pairwise comparisons between communities. Sample sizes were: $n_{\text{pairwise comparisons}} = 533$, $n_{\text{ecosystem types}} = 12$, $n_{\text{functions}} = 14$.

Across ecosystem functions and mountain regions, variation in species richness and turnover increased the contribution of diversity to variation in ecosystem functioning at similar magnitudes ($\beta_{R\rightarrow Y} = 0.86$ [0.14—1.5, 95% CI], z = 2.5, P = 0.013; $\beta_{T\rightarrow Y} = 1.0$ [0.56—1.5, 95% CI], z = 4.9, P < 0.001; Table S1.5). However, the magnitude of the diversity effect mediated by variation in species richness and turnover varied among the individual ecosystem functions (Fig. 3). For example, the effect of diversity on biomass stocks of birds and decomposition by soil arthropods was positively related to variation in species richness on Mt. Kilimanjaro, but negatively in the Ecuadorian Andes (Fig. 3). Overall, variation in both species richness and turnover increased the diversity effect on ecosystem functioning for the majority of ecosystem functions (variation in species richness: 7 of 14 functions; species turnover: 8 of 14 functions; Fig. 3).

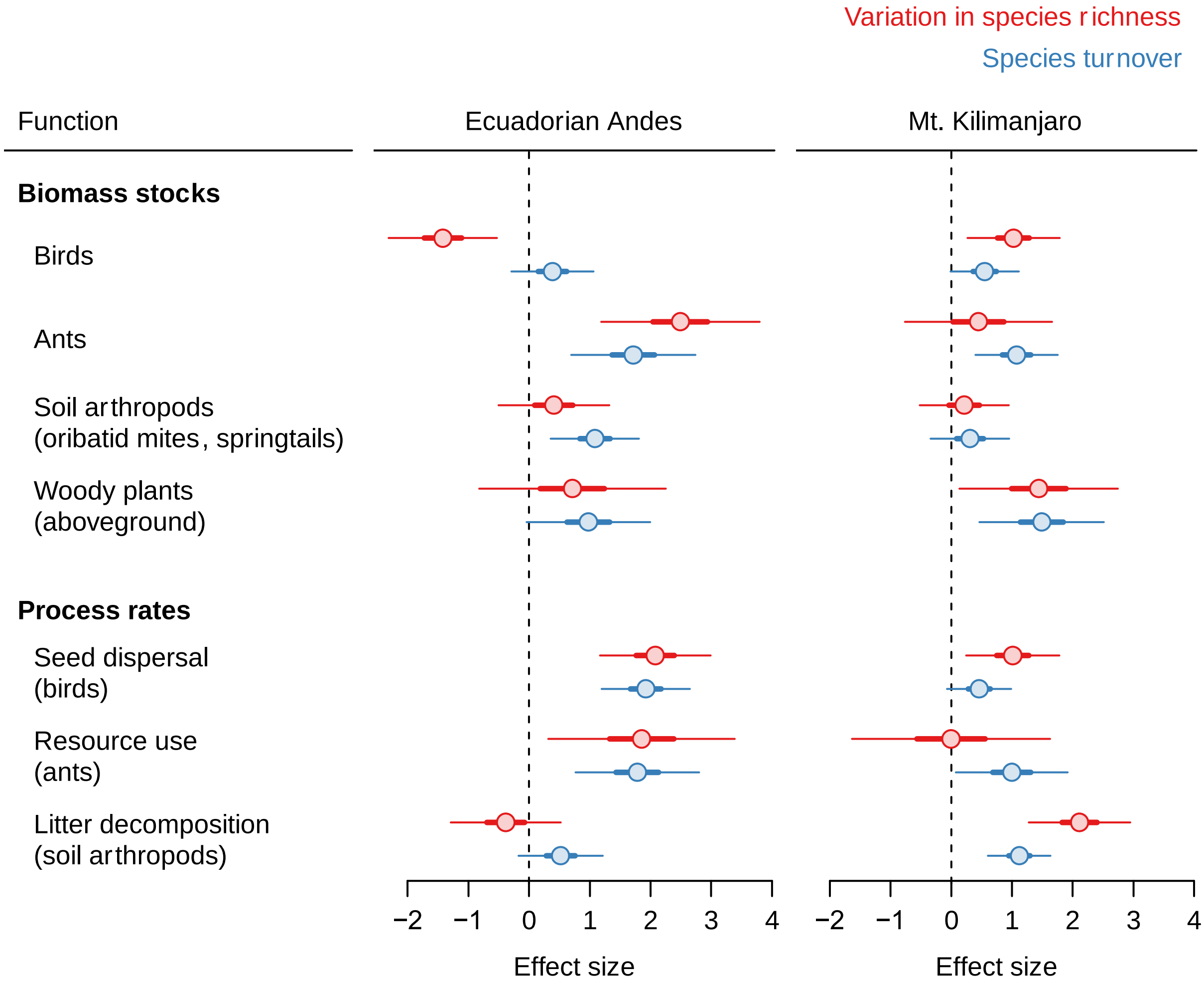

Figure 3. Effects of variation in species richness and species turnover on the diversity effect for individual ecosystem functions. Shown are random effect estimates (circles), as well as 50% and 95% Confidence Intervals (Cis, thick and thin lines, respectively) based on the MMMEMs for the effects of variation in species richness (blue) and species turnover

(green) on the contribution of diversity to variation in each ecosystem function (Table S1.5). The effect sizes reflect the expected change in the diversity effect for a 1% change in the predictor variable (for example, an effect of 2.0 means that an increase of 1% in the predictor variable causes an increase of 2% in the diversity effect). Sample sizes were: $n_{\text{observations}} = 533$, $n_{\text{ecosystem types}} = 12$, $n_{\text{functions}} = 14$.

We used a SEM to separate the direct and indirect effects of environmental heterogeneity on the contribution of diversity to ecosystem functioning across the two mountain regions (Fig. 4). Supporting our second hypothesis, we found that the increase in the diversity effect with environmental heterogeneity was solely mediated by variation in species richness ($\beta_{H \rightarrow R}$ = 0.64 [0.26—1.0, 95% CI], z = 3.4, P < 0.001), but not by species turnover ($\beta_{H \rightarrow T}$ = 0.10 [-0.26—0.45, 95% CI], z = 0.59, P = 0.56; Fig. 4; Table S1.5). Environmental heterogeneity did not directly increase the diversity effect ($\beta_{H \rightarrow Y}$ = 0.20 [-0.37—0.74, 95% CI], z = 0.72, P = 0.47), indicating that effects of environmental heterogeneity on ecosystem functioning were primarily driven by differences in species richness among communities.

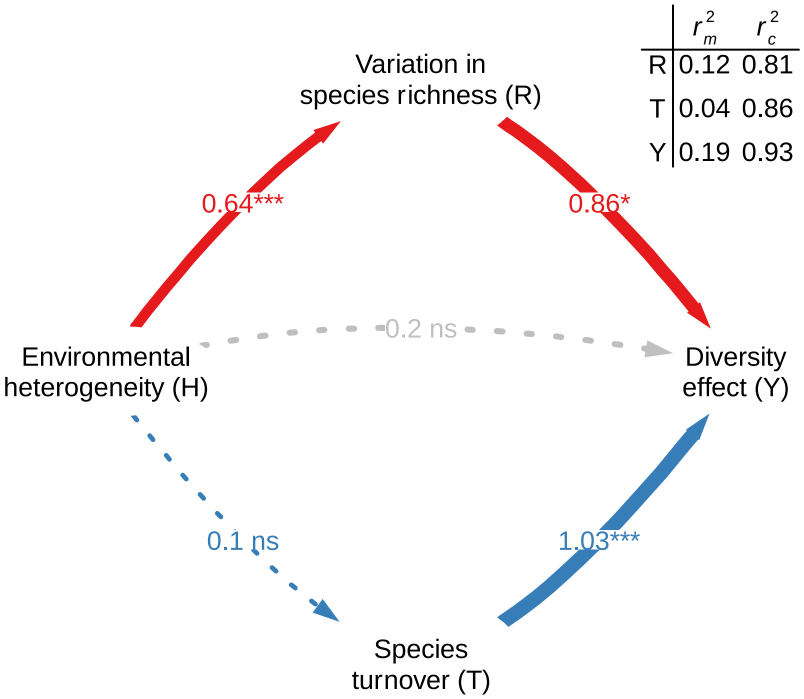

Figure 4. Structural equation model quantifying the direct effects of environmental heterogeneity on the contribution of diversity to variation in ecosystem functioning, as well as the indirect effects mediated by variation in species richness and species turnover (Table S1.5). The effect sizes reflect the expected change in the response variable for a 1% change in the predictor variable (for example, an effect of $\beta_{R \rightarrow Y} = 0.86$ means that an increase of 10% in variation in species richness across ecosystem types causes an increase of 8.6% in the diversity effect). Solid lines and asterisks indicate significant effects (*P < 0.05, ***P < 0.001), whereas dashed line and ns indicate non-significant effects (P > 0.05). R^2m, marginal R^2 considering only the variance explained by the fixed effects. R^2c, conditional R^2 considering the variance explained by both the fixed and random effects. Models are based on data from the Ecuadorian Andes and from Mt. Kilimanjaro in Tanzania. Sample sizes were: $n_{observations} = 533$, $n_{ecosystem\ types} = 12$, $n_{functions} = 14$.

Discussion

We here expand an analytical framework to quantify the contributions of variation in species richness and turnover to variation in ecosystem functioning along continuous environmental gradients at large spatial scales. By applying the framework to data from two mountain regions, we showed the contribution of diversity to variation in ecosystem functioning (i.e. the diversity effect) increased with increasing environmental heterogeneity. Moreover, we found that variations in both species richness and turnover contribute to the diversity effect. However, the increase in the diversity effect with environmental heterogeneity was solely mediated by variation in species richness among communities because species turnover was unrelated to environmental heterogeneity in our study systems.

The diversity effect increases with environmental heterogeneity

We found a consistent increase in the diversity effect with increasing environmental heterogeneity on both mountains. This finding is consistent with previous studies reporting an increase in the importance of biodiversity for ecosystem functioning in heterogeneous environments (e.g. Albrecht et al., 2021; Martinez-Almoyna et al., 2019). The generally lower diversity effect within a given ecosystem type suggests that variation in ecosystem functioning within ecosystem types is primarily driven by variation in the abundance or performance of specific species rather than by variation in species richness or turnover (Winfree et al., 2015). Such relationships have been documented across different ecosystem functions and ecosystems (Dangles & Malmqvist, 2004; Smith & Knapp, 2003; van der Plas, 2019) and suggest that the identity of abundant species in ecological communities is a main driver of ecosystem functioning (Dangles & Malmqvist, 2004; van der Plas, 2019). This is also in line with the observation from experiments that ecosystem functioning in single years and sites is often driven by a few dominant species (Isbell et al., 2011, 2018) that exploit the available resources efficiently (Allan et al., 2011). However, recent work has highlighted that positive relationships between species diversity and ecosystem functioning are less pronounced and can be negative for rare and non-native species (Dee et al., 2023). Nevertheless, the importance of biodiversity for ecosystem functioning has been documented in previous studies at large spatial and long temporal scales (Gonzalez et al., 2020; Isbell et al., 2011). Understanding the contribution of diversity to ecosystem functioning is particularly relevant for planning conservation measures at the scales of entire landscapes or larger regions. Our framework provides new means to quantify the contribution of diversity to variation in ecosystem functioning in natural ecosystems at such scales.

We found that the different contributions of diversity to ecosystem functioning within and across ecosystem types can be attributed to both changes in species richness and turnover. This suggests that the diversity effect was likely driven by two non-exclusive processes. First, variation in ecosystem functioning can be driven by species sorting, if environmental heterogeneity selects for species and species combinations that perform best under certain environmental conditions (Leibold et al., 2017). Effects of species sorting on ecosystem functioning would then arise if species turnover between ecosystem types also results in differences in the magnitude of ecosystem functioning between ecosystem types. In this case, species are complementary in their contributions to ecosystem functioning across ecosystem types (Isbell et al., 2011, 2018; Loreau et al., 2021), and differences in ecosystem functioning are then determined by the performance of these species under particular environmental conditions.

Second, species richness is likely to increase ecosystem functioning by assembly processes that facilitate species coexistence (Grace et al., 2016; Harpole et al., 2016). In particular, more favorable environmental conditions, for instance in terms of soil suitability or climatic conditions, at low compared with high elevations may allow more species to coexist (Grace et al., 2016). In this case, variation in ecosystem functioning is expected to increase because environmental heterogeneity drives variation in species richness among ecological communities (Grace et al., 2016). Our findings indicate that both of these are driving variation in species richness along the elevational gradients of the two mountain regions, but that the relative importance can vary depending on the type of ecosystem function. For example, the negative relationship of biomass stocks of birds and decomposition by soil arthropods to the variation in species richness in the Ecuadorian Andes compared to Mt. Kilimanjaro suggests that the relationship between species richness and ecosystem function can be context-dependent. For birds, the negative relationship in the Andes might reflect a scenario where high species richness leads to increased competition or resource partitioning, which could reduce biomass stocks. In contrast, on Kilimanjaro, higher species richness might enhance biomass through complementary resource use or reduced competition. Similarly, for soil arthropods, the negative relationship with decomposition in the Andes might indicate that increased species richness leads to less efficient decomposition processes, possibly due to different climatic conditions, soil properties, and/or arthropod community dynamics in the Andes compared to Kilimanjaro. Overall, these specific examples highlight the complexity of biodiversity-ecosystem function relationships and the importance of considering regional differences and the ecological context when assessing the relationship between species richness and ecosystem functions. Future studies could investigate the potential causes of differences in the relative importance of variation in species richness and turnover for the diversity effect between functions or groups of organisms.

Our study shows that variation in species richness and turnover increased the contribution of diversity to variation in ecosystem functioning across different mountain regions. While these findings suggest a relationship between biodiversity and ecosystem functioning, we acknowledge the limitations inherent in observational studies when inferring causality. It may be possible that underlying factors like environmental productivity (i.e. higher resource availability leading to greater abundances of organisms) have influenced both species and ecosystem functioning. Although the structural equation models revealed clear and consistent associations between biodiversity and ecosystem functioning for both mountain systems, we cannot fully rule out alternative explanations or reversed causality. To establish causality more robustly, future research should combine experimental approaches with observations to disentangle the effects of species richness, abundance, and environmental factors on ecosystem functioning.

We found that changes in species richness were the main driver of the larger contribution of diversity to ecosystem functioning along the continuous environmental gradient. This suggests that assembly processes related to species coexistence thereby influencing species richness play a more prominent role in driving ecosystem functioning across broad environmental gradients and in heterogeneous environments than assembly processes related to species sorting (Albrecht et al., 2021). Mechanisms of species coexistence are promoted in heterogeneous environments (Tredennick et al., 2017). Thus, the importance of species richness may be particularly pronounced in highly diverse and environmentally heterogeneous tropical ecosystems, such as the ones studied here. Previous work in tropical and temperate regions provides inconsistent results regarding the relative importance of variation in species richness and turnover for variation in ecosystem functioning at large spatial scales (Barnes et al., 2016; Brose & Hillebrand, 2016; Winfree et al., 2018; Dainese et al., 2019). While a previous analysis suggests that species richness best predicts ecosystem functioning at large spatial scales both in temperate and tropical ecosystems (Barnes et al., 2016), other work suggests that species turnover is more important for promoting ecosystem functioning (Winfree et al., 2018). Our study shows that environmental heterogeneity was not related to species turnover. This is surprising because other studies have shown such relationships (Gianuca et al., 2017; Jiang et al., 2023). This discrepancy could be explained by other ecological processes, such as dispersal limitation or historical legacies, that might primarily drive species turnover across the studied environmental gradients (González-Trujillo et al., 2021; Wang et al., 2013). In confirmation of our findings, previous studies of plant and bird communities in the Andes and on Mt. Kilimanjaro also showed that environmental heterogeneity was related to abundance and richness differences of plants and birds within and between elevations (Barczyk et al., 2023; Ferger et al., 2017).

An analytical framework to quantify contributions of diversity to ecosystem functioning

Our framework is able to quantify the importance of variation in species richness and turnover for changes in ecosystem functioning at large spatial scales. However, it cannot untangle the contributions of dispersal or species interactions as drivers of the underlying community assembly processes (Jiao et al., 2019; Wang et al., 2013). Yet, the framework could be extended by integrating traits as species-specific predictors of the functional contributions to ecosystem functions. More specifically, trait spaces of plants and animals could be used to quantify how changes in functional diversity and composition between communities would affect ecosystem functioning (e.g. Junker et al., 2023). Such an extension could link the framework to assembly processes associated with species differences in life-history strategies (e.g. Junker et al., 2023), metabolic demands (Brown et al., 2018), or dispersal (Wang et al., 2013). This could allow us to quantify the magnitude of trait change in relation to species richness and turnover and thus provide a more mechanistic understanding of the contribution of diversity to ecosystem functioning in different communities.

Our proposed framework provides new possibilities to quantify BEF relationships at large spatial scales and is applicable to data on ecosystem functioning for any type or number of ecosystem types. It extends beyond previous work contrasting BEF relationships only within the same or across ecosystem types (Albrecht et al., 2021) to comparisons among naturally assembled communities along continuous environmental gradients. As such, it allows comparisons at landscape- or regional scales which are most relevant for conservation planning. This is timely because the increasing availability of biodiversity and ecosystem function data from large-scale projects in natural environments will enable the application of the framework to different biomes (e.g. Drescher et al., 2016). By proposing this framework, we call for future studies that quantify the contribution of diversity to ecosystem functioning across different biomes. Our study from two tropical mountains is a first step in that direction and shows how new conceptual frameworks can be used to analyse biodiversity-ecosystem functioning relationships at large spatial scales.

Author contributions

N.F., M.S., E.L.N., R.B., J.A. and A.W. conceptualized the idea of this manuscript. J.A. and A.W. wrote the first draft with input from N.F., E.L.N., R.B. and M.S. A.W. & J.A. led the writing of the manuscript.

K.B.G., M.F., A.H. and I.S.-D. initiated the research unit at Mt. Kilimanjaro.

J.B. & N.F. initiated the research unit in Ecuador

J.B., R.B., K.B.G., N.F., M.F., A.H., J.H., R.K., Y.K., C.L., E.L.N., M.K.P, S.S., I.S.-D., M.S., A.V., W.W. conceptualized and supervised the data collection.

J.A. and A.W. developed the analytical tools.

J.A. analyzed and visualized the data.

All other authors commented on the manuscript and gave final approval for publication.

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Data accessibility statement

All data and code supporting the results of the study will be made publicly available on figshare upon acceptance of the manuscript.

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Appendix

Methods: Study area

The **Ecuadorian Andes** have been formed by tectonic activity whereby the subduction of the Pacific plate under the continental plate uplifted the mountain cahin with its origin in the early Miocene or earlier (Evenstar et al., 2015).

In the Ecuadorian Andes, the data was collected at three sites in southern Ecuador located in and next to the Podocarpus National Park (PNP) (Beck et al., 2019, Bendix et al. 2021). Here, the annual mean temperature ranges between 19°C and 13°C (Bendix et al., 2006; Richter, 2003). The study sites experience a tropical humid climate with annual precipitation ranging from approximately 2,300 mm at 1,850 m a.s.l. to over 6,000 mm at 3,100 m a.s.l (Bendix et al., 2006). The wet season, which is exceptionally moist, occurs from April to July, while a period with less precipitation extends from September to December. The central research station is located in the valley of Rio San Francisco (Estación Científica San Francisco; Lat. 3°58’18’’ S (-3.971667), Long. 79°4’45’’ W (-79.079167); Beck et al., 2019). Study sites with premontane rainforest (at elevations of ~1,000 m a.s.l.) were located at the Bombuscaro area within PNP. Study sites with montane rainforest (at elevations of ~2,000 m a.s.l.) were located at the humid eastern slopes of the main Cordillera, in the valley of the Rio San Francisco at the border of the PNP (Reserva Biológica San Francisco). Study sites at the upper montane sites (elevations of ~3,000 m a.s.l.) were located at the Cajanuma area of PNP. Study sites in disturbed forests were located on private land next to the PNP, mostly embedded in pastures, pasture successions with southern bracken fern or exotic tree plantations (pines) (Curatola Fernández et al., 2015; Knoke et al., 2014, 2016).

Mt. Kilimanjaro is a dormant volcano from the Pleistocene or earlier covering multiple climatic and cultivation zones (G. W. van der Plas et al., 2021; Wilcockson, 1956). Here, data was collected at the southern and southeastern slopes (Tanzania, East Africa; 2° 45′–3° 25′ S, 37° 00′–37° 43′ E) (Peters et al., 2019b). Mt. Kilimanjaro covers lowlands with elevations of 700 m a.s.l. to a snow-capped summit with an elevation of 5,895 m a.s.l. However, for this study, we focused on elevations up to ~3,000 m a.s.l. The mean annual temperature ranges depending on the elevational level between 25°C to -8°C (Peters et al., 2019a). The mean annual precipitation peaks at ~2,200 m a.s.l. with 2700 mm (Hemp, 2006c). Mt. Kilimanjaro is characterized by a rainy season that lasts from March to May and short rains in November (Hemp, 2006b; Peters et al., 2019a). Mt. Kilimanjaro has been characterized for a long time by land use and thus natural ecosystem types (in particular in the lowlands) have been degraded by fire, wood extraction, and agroforestry practices (Hemp, 2006b, 2006d). Only the area above 1,800 m a.s.l. is protected and has been designated as a national park (Mt. Kilimanjaro National Park; (Hemp, 2006e; Peters et al., 2019a).

Methods: Study design

Data was collected on 15 to 67 study sites (median = 18 study sites) in the **Ecuadorian Andes**, south-eastern Ecuador, and 12 to 30 study sites (median = 29 study sites) on **Mt. Kilimanjaro**, Tanzania. In both mountain regions, we covered an elevational gradient of approximately 1,000-3,000 m.a.s.l. In the **Ecuadorian Andes**, data was collected in undisturbed premontane forest and disturbed premontane forest at elevations of 960–1,268 m a.s.l., in undisturbed lower montane forest and disturbed lower montane forest at elevations of 1,850–2,450 m a.s.l. as well as in undisturbed upper montane forest and disturbed upper montane forest at elevations of 2,679–2,931 m a.s.l. (Supplementary Methods Table 1). At **Mt. Kilimanjaro**, Tanzania, sampling was performed in undisturbed and disturbed lower montane forest (i.e., chagga home gardens) at elevations of 1,171–2,097 m a.s.l., undisturbed and disturbed *Ocotea* forest at elevations of 2,150–2,741 m a.s.l., *Podocarpus* forest at elevations of 2,720-2,970 m a.s.l. as well as in undisturbed and disturbed podocarpus forest at elevations of 2,753–3,009 m a.s.l. (Supplementary Methods Table 1).

Methods: Environmental variables

The methods for measuring the environmental variables in this study were previously explained in detail. We offer a concise summary with a reference to the respective publications (Appelhans et al., 2016; Peters et al., 2019a).

Methods: Soil variables

In the **Ecuadorian Andes**, soil properties were determined to represent the upper 0.5 m of the mineral soil. Two sampling designs were used depending on the location: Soils were sampled from three profiles on 18 study sites along the elevation gradient from 1,000-3,000 m a.s.l. and at 8-10 profiles along transects in four micro-catchments at 1,900-2,200 m a.s.l. Soil profiles were excavated down to 1 m depth and representative samples were taken from each horizon of the mineral soil. The samples were dried at 40 °C, sieved to <2 mm and an aliquot milled in a planetary ball mill (PM400, Retsch, Haan, Germany). Total C and N content were measured by elemental analysis (Flash 2000 HT Plus, Thermo Scientific, Bremen, Germany) via thermal combustion at 1020 °C. The total P content was determined after microwave digestion (Mars 6, CEM, Kamp-Lintfort, Germany) with HNO_3, H_2O_2, and HF by ICP-OES (5100 OES VDV, Agilent Technologies, Waldbronn, Germany). We calculated a weighted average of the measured element contents to 0.5 m mineral soil depth by taking into account the thickness and density of each soil layer. Because the soils were free of carbonates, total C corresponds to organic carbon (C_{org}). To determine the content of soil organic carbon at **Mt. Kilimanjaro**, samples of the organic horizon and the mineral soil (0-5cm) were collected at five locations per study site. Mineral soil and organic horizon materials were air-dried until constant weight. Soil was sieved to 2 mm with visible root fragments being further removed, while the organic horizon material was shredded prior to grinding with a mixer mill (MM200, Retsch, Haan, Germany) (Peters et al., 2019a). All samples were analyzed using dry combustion elemental analyzer (Flash EA1112, Thermo Scientific, Bremen, Germany) to determine the C content (i.e., C_{org}, because all soils were carbonate-free) at 950 °C. Individual element contents of soil and the organic layer were averaged across the five locations for each study site. To quantify the C/N and N/P ratios, mineral soil samples were collected from soil pits at 10 cm intervals using a standard soil auger. Mineral soil samples were dried at 60 °C for 24 h and root and plant manterials removed by sieving to < 2 mm before grinding them for further analysis. The total C and N concentratons of the soils were measured using an elemental analyzer (Vario EL, Elementar) at 950 °C.

The total P content was determined using inductively coupled plasma optical emission spectrometry (Spectro Analytical Instruments) after pressure digestion with concentrated HNO_3 .

Methods: Climate variables

In the **Ecuadorian Andes**, temperature and precipitation information was gathered for each 1-ha site. The average monthly temperature (i.e., the monthly mean of daily mean temperatures) was acquired using an air temperature regionalization tool developed specifically for the study region (Fries et al., 2012). Monthly mean precipitation (i.e., the average of the monthly precipitation sum) was gathered with a hybrid approach blending ground-based and space-born remote sensing data (using local area weather radar and satellite imagery) with observation data of the meteorological gauge network (Rollenbeck & Bendix, 2011, Bendix et al. 2017).

To assess the climatic conditions at the study sites at **Mt. Kilimanjaro,** mean annual temperature and mean annual precipitation was assessed. To measure annual temperature, we installed temperature sensors approximately 2 meters above the ground at all study sites (Peters et al., 2019a). The sensors recorded temperature at 5-minute intervals for about 2 years. The mean annual temperature (°C) was calculated by averaging all the measurements per study site. Mean annual precipitation (mm yr^{-1}) was estimated by interpolating a 15-year dataset from a network of about 70 rain gauges on Mt. Kilimanjaro using a co-kriging approach (Appelhans et al., 2016; Peters et al., 2016).

Methods: Ecosystem functions

In each mountain region, data on seven ecosystem functions belonging to either biomass stock or process rates were collected (Supplementary Methods Table 2). We were able to directly measure the species-specific functional contributions for 5 out of 7 functions in each community. However, we did not have direct estimates for the functional contributions of litter decomposition by oribatid mites and springtails. Instead, we assumed that the functional contribution of a species was proportional to its relative abundance or biomass at each site.

Methods: Biomass stocks

To determine the **biomass stocks** of **springtails, oribatid mites, ants, and birds** in the **Ecuadorian Andes** and at **Mt. Kilimanjaro** at each study site, we combined data on species abundances with data on species-specific per capita mass. Species abundances at each study site were assessed using standardized methods with taxon-specific sampling techniques, which have been detailed in previous studies (for Ecuador: Marian et al., 2018; Santillán et al., 2018; Tiede et al., 2017; for Kilimanjaro: Peters et al., 2016). To estimate the per capita mass for birds, we used existing literature (Dunning, 2008; Wilman et al., 2014). For ants and springtails, we applied allometric equations to morphometric measures (i.e., head length for ants, and total body length for springtails) to derive species-specific estimates of per capita mass. Morphometric measurements were taken from up to ten randomly selected individuals per species using a binocular microscope with a calibrated ocular micrometer. The individual biomass estimated using allometric equations closely matched the true biomass determined with a precision scale.

In the **Ecuadorian Andes**, we included only trees (no shrubs) with a diameter at breast height greater than or equal to 10 cm (Homeier & Leuschner, 2021). We used basal area as a proxy for aboveground biomass (AGB). We calculated the species-specific basal area by summing the individual basal area measurements for each species at each study site. To determine the aboveground **biomass stocks** of **woody plants** at **Mt. Kilimanjaro**, we included all woody plant individuals that were taller than 1.3 m and had a diameter at breast height greater than or equal to 10 cm (trees) or less than 10 cm (shrubs) (Ensslin et al., 2015). We applied pantropical allometric equations to measures of plant height, diameter at breast height, and wood density (Ensslin et al., 2015). We calculated species-specific aboveground biomass stocks by summing individual biomass estimates for each species at each study site.

Methods: Process rates

To measure seed dispersal by birds, resource use by ants, and litter decomposition by microorganisms, process-specific protocols were used. The approach for **seed dispersal** measurement by birds followed standardized methods, which have been previously described in the literature (Ecuador: Quitián et al., 2018; Mt. Kilimanjaro: Albrecht et al., 2018). In the **Ecuadorian Andes** as well as at **Mt. Kilimanjaro**, bird-fruit interactions were monitored on a site measuring 30 m x 100 m at each study site. Birds were observed over four consecutive days, for a total of 25 hours, using binoculars to record interactions with fruiting plants. For each bird species, the number of visits to each fruiting plant species was recorded, as well as their behavior. We calculated species-specific contributions to seed dispersal as the number of visits to all fruiting plants by each bird species, considering only those visits that involved legitimate seed removal events, such as swallowing or carrying away fruits from the mother plants.

To assess **resource use by ants**, bait experiments were conducted at each study site. In the **Ecuadorian Andes**, six 50 ml Falcon tubes were used at five subplots, respectively (Tiede et al., 2017). At **Mt. Kilimanjaro**, thirty 50 ml Falcon tubes were placed along three 50-m transects at ground level (Peters et al., 2014). In the Ecuadorian Andes, each tube contained 15 mL and at **Mt. Kilimanjaro** 10 mL of nutrient solutions, such as sugar, sugar-protein, protein, water, salt, or oil, with five replicates per nutrient. In the **Ecuadorian Andes**, ant data was collected at 1,000, 1,500, 2,000, 2,500, and 3,000 m a.s.l. after 2, 3, 4, 4.5, and 5 hours, respectively. Based on the occurrence of ants at the baits, the species-specific contributions to resource use were calculated as the proportion of baits detected by each ant species. In cases where more than one ant species was recorded at a bait, we assigned species-specific contributions to resource use in proportion to the relative abundance of each ant species at that bait. At **Mt. Kilimanjaro**, the baits were collected after two hours and the number of individuals of each ant species that were present at each bait were recorded.

To study net **litter decomposition rates**, standardized litter bags with leaves or roots (with a 4 mm mesh and containing 10 g of leaves or roots) were utilized in the **Ecuadorian Andes**. 120 litterbags were placed at each study site, with one at each elevational level, and collected after 6, 12, 24, 36, and 48 months. We followed an established protocol to process the leaves and roots (Marian et al. 2017). Decomposition rates were calculated based on the remaining carbon (CR) in the litterbags at the sampling dates (n) expressed as a percentage of the initial amount of carbon placed in the litterbags (C0). Changes in the remaining nitrogen (NR) were similarly expressed as a percentage of the initial amount of nitrogen placed in the litterbags (N0). We used the following formulas: $CR\ [\%] = (Cn/C0) \times 100$ and $NR\ [\%] = (Nn/N0) \times 100$, with Cn and Nn being the amount of carbon and nitrogen remaining at each sampling date n. We calculated the contents of carbon (CC) and nitrogen (NC) in the litter using the following equations: $CC\ [\%] = (Cn/DWn) \times 100$ and $NC\ [\%] = (Nn/DWn) \times 100$, with DWn being the dry weight of litter remaining at sampling date n.

At **Mt. Kilimanjaro** litter decomposition rates were assessed using litterbags filled with dried maize straw (10 cm x 15 cm, 20 µm x 20 µm mesh size, and containing 5 ± 0.05 g of maize husks; Peters et al., 2019). Three bags were placed at each study site and collected after 69 to 86 days. To process the leaves, established protocols were applied. Due to logistical reasons, bags at lower elevations were exposed for a longer time than bags at higher elevations. To adjust for these differences, decomposition rates per day were calculated using the equation $k = -\ln(m_{LOI} / m_{OAF}) / t$, where m_{LOI} is the weight after loss-on-ignition, m_{OAF} is the original ash-free weight, and t is the number of days the bags have been exposed. The decomposition rates per study site were averaged.

In both the **Ecuadorian Andes** and at **Mt. Kilimanjaro**, we did not have direct measures of species-specific contributions to litter decomposition. Thus, we estimated the specific contribution of each species to decomposition at each site based on the relative abundance of each species at that site. In the **Ecuadorian Andes**, decomposition rates were related to the abundance of oribatid mites (Marian et al., 2018) and at **Mt. Kilimanjaro** to springtails (Peters et al., 2016).

Tables S1.1- S1.5

Table S1.1: Overview of the seven ecosystem functions belonging to biomass stocks or process rates and the number of study sites (n) per function for Ecuadorian Andes (E) and Mt. Kilimanjaro, Tanzania (T).

code	taxon_variable	function category	region	n
ER02	mite decomposition	process rate	E	27
ER03	ant resource use	process rate	E	15
ER04	bird seed dispersal	process rate	E	17
ES01	woody plant aboveground biomass	biomass stock	E	67
ES02	oribatid mite biomass	biomass stock	E	27
ES03	ant biomass	biomass stock	E	15
ES04	bird biomass	biomass stock	E	18
TR02	springtail decomposition	process rate	T	30
TR03	ant resource use	process rate	T	12
TR04	bird seed dispersal	process rate	T	29
TS01	woody plant aboveground biomass	biomass stock	T	24
TS02	springtail biomass	biomass stock	T	30
TS03	ant biomass	biomass stock	T	12

Table S1.2: Overview of the studied ecosystem types in the **Ecuadorian Andes** (more details in Gottlicher et al., 2009; Homeier et al., 2008) and at Mt. Kilimanjaro (more details in Peters et al. 2019).

Mountain region	Ecosystem type	Description
Ecuadorian Andes	premontane forest	~800-1,300 m a.s.l., continuous humid & evergreen premontane forest with up to 40m canopy height (Homeier et al., 2008)
	disturbed premontane forest	~1,000 m a.s.l., fragmented premontane forest bordering pastures used for grazing
	lower montane forest	~1,300- 2,100 m a.s.l., continuous humid & evergreen lower mountain forest with up to 30m canopy height (Homeier et al., 2008)
	disturbed lower montane forest	~2,000 m a.s.l., fragmented lower mountain forest bordering pastures used for grazing

	upper montane forest	~2,100- 2,700 m a.s.l. , continuous and humid upper montane forest with up to 25 m canopy height (Homeier et al., 2008)
	disturbed upper montane forest	~3,000 m a.s.l., fragmented upper montane forest bordering pastures used for grazing
Mt. Kilimanjaro	lower montane forest	1,560-2,040 m a.s.l., natural *Cassipourea* forests on the northern slope and *Agarista–Syzygium–Ocotea* forests on the southern slopes (Hemp, 2006e)
	chagga home garden	1,169-1,788 m a.s.l., anthropogenic, agroforestry systems with coffee and banana trees, characterized by a diverse vegetation structure with trees, shrubs, lianas, epiphytes and herbs (Hemp, 2006a)
	Ocotea forest	2,120-2,750 m a.s.l., natural Camphor forests dominated by *Ocotea usambarensis*, rich in

		vascular epiphytes and tree ferns (Hemp, 2006e)
	disturbed *Ocotea* forest	2,220-2,560 m a.s.l., anthropogenic, Ocotea forest undergoing intensive illegal logging of camphor trees (Hemp, 2006e)
	Podocarpus forest	2,720-2,970 m a.s.l., natural forest dominated by the gymnosperm *Podocarpus latifolius* (Hemp, 2006e)
	disturbed *Podocarpus* forest	2,770-3,060 m a.s.l., anthropogenic, Podocarpus forest disturbed by fire (Hemp, 2006e)

Table S1.3: Summary of multiple membership mixed effects model (MMMEM) assessing the relationship between environmental heterogeneity and the diversity effect based on data from the Ecuadorian Andes and Mt. Kilimanjaro. The model included correlated random factors for intercepts and slopes to account for variation in the relationship between the diversity effect (Y) and environmental heterogeneity (H) between ecosystem functions. In addition, the model included a multiple-membership random-effects structure, to account for non-independence of pair-wise comparisons involving the same ecosystem types (see Methods section). Region identity (Ecuadorian Andes and Mt. Kilimanjaro) was included as a fixed factor. Models including interaction terms between the predictor variables and region were not supported by the data (see Supplementary Table 4). Sample sizes were: $n_{\text{observations}} = 533$, $n_{\text{ecosystem types}} = 12$, $n_{\text{functions}} = 14$. Y= Diversity effect. R^2_m = Ma*rginal* R^2 considering only the variance of the fixed effects (without the random effects). R^2_c = *conditional* R^2 considering both the fixed and random effects.

Fixed effects					Random effects		
							Correlation
Source of variance	Estimate	SE	z	P	Source of variance	SD	Intercept|id
Y ~							
Intercept	0.47	0.093	5.1	< 0.001	Intercept|id	0.26	
H	1.1	0.24	4.4	< 0.001	H|id	0.79	-0.63
Region	-0.11	0.11	-0.94	0.35			
R^2_m	0.13				Intercept|MM(Type)	0.039	
R^2_c	0.84				Residual	0.10	

Table S1.4: Summary of model selection for the models assessing the relationship between environmental heterogeneity (H) and the diversity effect (Y) based on data from the Ecuadorian Andes and Mt. Kilimanjaro. Shown are comparisons between a model including only the effect of Region; a model including the effects of Region and environmental heterogeneity; as well as a model including the effects of Region, environmental heterogeneity and their interaction.

Model	df	logLik	BIC	delta	weight
Y ~					
H + Region	8	402.2	-754.3	0	0.938
H * Region	9	402.7	-748.8	5.43	0.062
Region	5	334.6	-637.8	116	0

Table S1.5: Summary of structural equation model based on multiple membership mixed effects models (MMMEMs) assessing the effects of environmental heterogeneity (H), variation in species richness (R), and species turnover (T) on the diversity effect (Y) based on data from the Ecuadorian Andes and Mt. Kilimanjaro. The models included correlated random factors for intercepts and slopes to account for variation in the relationships between the response and predictor variables between ecosystem functions. In addition, the models included a multiple-membership random-effects structure, to account for non-independence of pair-wise comparisons involving the same ecosystem types. Region identity (Ecuadorian Andes and Mt. Kilimanjaro) was included as a fixed factor. Models including interaction terms between the predictor variables and region were not supported by the data (see Supplementary Table 4). Sample sizes were: $n_{\text{observations}} = 533$, $n_{\text{ecosystem types}} = 12$, $n_{\text{functions}} = 14$. Y= diversity effect. H, environmental heterogeneity; R, variation in species richness; T, species turnover. R^2_m, Ma*rginal* R^2 considering only the variance explained by the fixed effects. R^2_c*, conditional* R^2 considering the variance explained by both the fixed and random effects.

Fixed effects					Random effects				
							Correlation		
Source of variance	Estimate	SE	z	P	Source of variance	SD	Intercept|id	H|id	R|id
(**a**) Y ~									
Intercept	-0.19	0.16	-1.2	0.24	Intercept|id	0.49			
H	0.20	0.27	0.72	0.47	H|id	0.91	0.51		
R	0.86	0.34	2.5	0.013	R|id	1.2	-0.84	-0.70	
T	1.0	0.21	4.9	< 0.001	T|id	0.65	-0.80	-0.67	0.71
Region	0.011	0.11	0.098	0.92					
R^2_m	0.19				Intercept|MM(Type)	0.042			
R^2_c	0.93				Residual	0.073			
(**b**) R ~									
Intercept	0.15	0.025	6.0	< 0.001	Intercept|id	0.062			

H	0.64	0.19	3.4	< 0.001	H|id	0.64	-0.62
Region	0.038	0.031	1.2	0.21			
R^2_m	0.12				Intercept|MM(Type)	0.031	
R^2_c	0.81				Residual	0.060	
(**c**) T ~							
Intercept	0.47	0.051	9.1	< 0.001	Intercept|id	0.14	
H	0.10	0.17	0.59	0.56	H|id	0.59	-0.55
Region	-0.057	0.065	-0.88	0.38			
R^2_m	0.037				Intercept|MM(Type)	0.034	
R^2_c	0.86				Residual	0.057	

Table S1.6: Summary of model selection for the models assessing the effects of environmental heterogeneity, variation in species richness, and species turnover on the diversity effect based on data from the Ecuadorian Andes and Mt. Kilimanjaro. Shown are comparisons between models including only the effect of Region; models including the effects of Region, Heterogeneity (H), Variation in species richness (R) and species turnover (T); as well as models including the effects of Region H, R, and T, as well as the interaction of Region with H, R, and T.

Model	df	logLik	BIC	delta	weight
(**a**) Y ~					
H + R + T + Region	17	539.9	-973.1	0	0.998
(H + R + T) * Region	20	543.0	-960.5	12.6	0.002
Region	5	334.6	-637.8	335	0
(**b**) R ~					
H + Region	8	679.5	-1308.9	0	0.948
H * Region	9	679.8	-1303.0	5.81	0.052
Region	5	599.6	-1167.9	141	0
(**c**) T ~					
H + Region	8	700.6	-1350.9	0	0.962
H * Region	9	700.5	-1344.4	6.48	0.038
Region	5	617.9	-1204.3	147	0

Table S1.7:. Summary of mixed effects model (MEM) assessing the raw relationship between species richness and ecosystem functioning based on data from the Ecuadorian Andes and Mt. Kilimanjaro. Overall, ecosystem functioning was positively related to species richness for all functions except one (resource use by ants in the Ecuadorian Andes). Before the analysis, we log-transformed the variables after standardizing the values of ecosystem functions and species richness (*S*) for each function by their mean values for a given function (*F*) (i.e., $S'_i = \log(S_i / \text{mean}(S_i))$ and $F'_i = \log(F_i / \text{mean}(F_i))$). The model included correlated random factors for intercepts and slopes to account for variation in the relationship between species richness and ecosystem functioning across functions. In addition, the model included a random factor for site identity. Sample sizes were: $n_{\text{observations}} = 353$, $n_{\text{site}} = 143$, $n_{\text{function id}} = 14$. R^2_m = M*arginal* R^2 considering only the variance of the fixed effects (without the random effects). R^2_c = *conditional* R^2 considering both the fixed and random effects.

Fixed effects					Random effects		
							Correlation
Source of variance	Estimate	SE	z	P	Source of variance	SD	Intercept|id
log(F) ~							
Intercept	-0.45	0.15	-3.0	0.0027	Intercept|id	0.35	
log(S)	1.1	0.30	3.6	< 0.001	log(S)|id	1.0	0.040
Region	0.18	0.21	0.84	0.40			
R^2_m	0.25				Intercept|plot	0.24	
R^2_c	0.62				Residual	0.73	

Table S1.8: Summary of model selection for the models assessing the raw relationship between species richness and ecosystem functioning based on data from the Ecuadorian Andes and Mt. Kilimanjaro. Shown are comparisons between a model including only the effect of Region; a model including the effects of Region and standardized and log-transformed species richness (log(S)), as well as a model including Region, log(S), and their interaction.

Model	df	logLik	BIC	delta	weight
log(F) ~					
log(S) + Region	8	-436.4	919.8	0	0.925
log(S) * Region	9	-436.0	924.8	5.03	0.075
Region	5	-569.6	1168.6	249	0

Figure S1.1-2

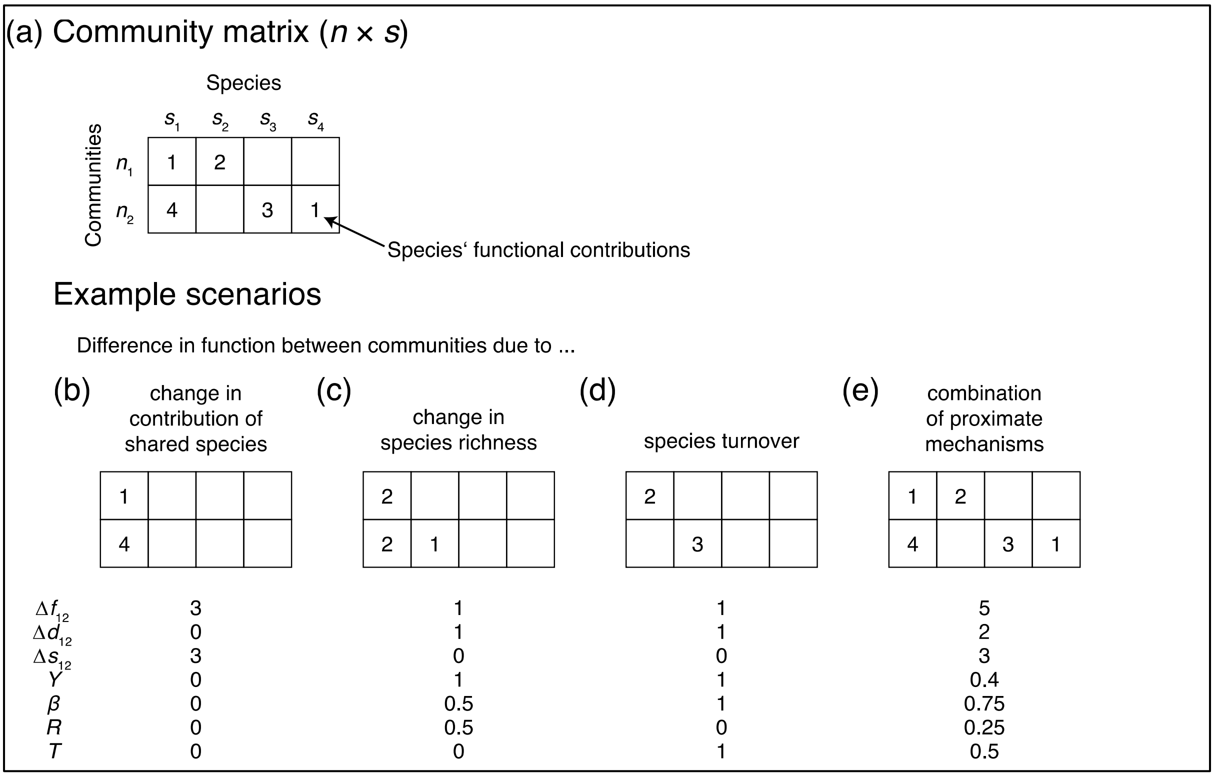

Fig. S1.1: Example scenarios of differences in ecosystem functioning between communities. (a) The matrix F (n × s) describes the functional contribution of s species (here s1, s2, s3 and s4) to ecosystem functioning in n communities (here n1 and n2). The approach therefore requires that the ecosystem function of interest comprises the summed functional contributions of individual species. The number in each cell depicts the magnitude of species' functional contributions to ecosystem functioning in each community. (b-e) Examples of how differences in ecosystem functioning between communities due to changes in the contribution of shared species (b), changes in species richness (c), species turnover (d) or a combination thereof (e) are captured by the diversity effect (Y) as well as by the species richness and turnover components of beta-diversity.

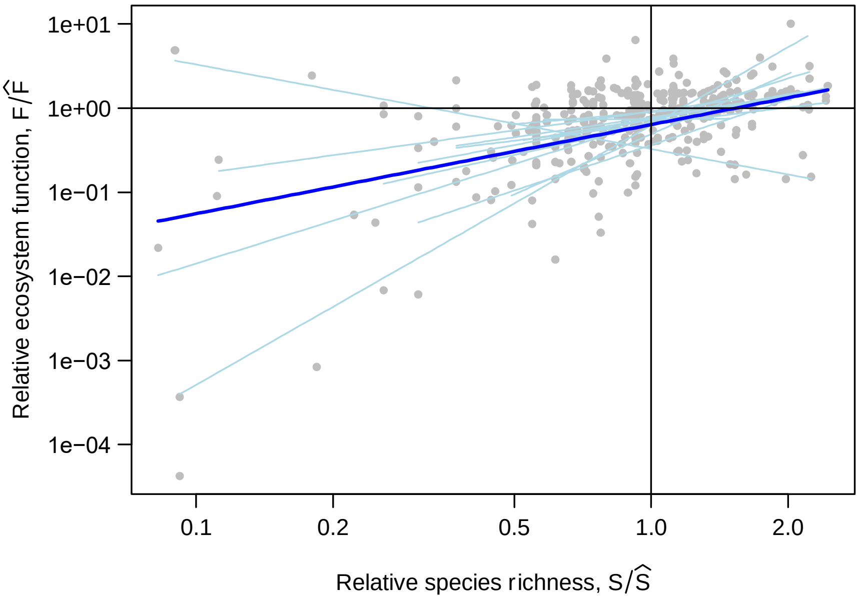

Fig. S1.2: Species richness–ecosystem function relationships across the 7 functions and 2 mountain regions. Individual relationships (light blue lines) and average relationships (dark blue line) are based on linear mixed-effects model (LMM). In this model, we treated the magnitude of the ecosystem functions (*F*) as the response variable and species richness (S) as the explanatory variable. Before the analysis, we log-transformed the variables after standardizing the values of ecosystem functions and species richness for each function by their mean values for a given function (i.e., S'_i = log(S_i / mean(S_i)) and F'_i = log(F_i / mean(F_i))). We included correlated random factors for intercepts and slopes to account for variation in the relationship between species richness and ecosystem functioning across functions. In addition, we included a random factor for site identity. The LMM was implemented in the *lme4* package (Bates et al., 2015). Gray points are raw data (n = 353). Note that there was one negative species richness–ecosystem function relationship (resource use of ants in Ecuador) that may be explained by colony-foraging of ants leading to the dominance of resources by one or a few species and the exclusion of other species at high levels of resource use. Note that the only negative relationship shown is the one for resource use of ants in the Ecuadorian Andes.