*Diversity and Distributions*

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# Effects of Species Richness and Turnover on Ecosystem Functioning in Heterogeneous Environments of Two Tropical Mountains

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## ABSTRACT

**Aim:** Progress has been made in understanding the relationship between biodiversity and ecosystem functioning (BEF) in both experimental and real-world ecosystems. Yet, we have a limited understanding of the extent to which biodiversity affects ecosystem functioning in heterogeneous environments and whether variation in ecosystem functioning between communities is related to variation in species richness or turnover. Here, we quantify the relative contribution of variation in species richness and species turnover to variation in ecosystem functioning between communities (i.e., the diversity effect) along two tropical elevational gradients.

**Location:** Andes (Ecuador) and Mt. Kilimanjaro (Tanzania).

**Taxa Studied:** Woody plants, springtails, soil arthropods, ants and frugivorous birds.

**Methods:** We collected data on seven ecosystem functions, including biomass and process rates, across six ecosystem types along the two elevational gradients. We then combine the ecological Price equation with the concept of β-diversity to quantify

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how the diversity effect is shaped by environmental heterogeneity within and across ecosystem types, and whether the effect of environmental heterogeneity is primarily mediated by variation in species richness or species turnover.

**Results:** The diversity effect on ecosystem functioning increased consistently with environmental heterogeneity on both mountains. Species richness and turnover, on average, contributed similarly to the diversity effect on ecosystem functioning in both mountain regions, but effect sizes varied across functions. The increase in the diversity effect with environmental heterogeneity was primarily mediated by species richness, while species turnover played a secondary role in mediating the effects of environmental heterogeneity.

**Main Conclusions:** Our study reveals that the diversity effect on ecosystem functioning increases with environmental heterogeneity and that species richness, rather than species turnover, primarily drives this relationship. The dominant role of species richness in mediating the effect of environmental heterogeneity indicates that BEF relationships along environmental gradients are strongly influenced by environmental filters that limit local species coexistence.

## 1 | Introduction

Global change is causing a substantial modification and reorganisation 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 species richness and ecosystem functioning are usually positively related (e.g., Brose and Hillebrand 2016). In these experiments, the effect of species loss on ecosystem functioning can be as strong as or even stronger than direct effects of environmental factors on ecosystem functioning (Hooper et al. 2012). In natural systems, however, the effect of species richness on ecosystem functioning is more difficult to quantify due to heterogeneity in environmental conditions and community composition and, hence, may be more variable than in small-scale experiments (van der Plas 2019). For instance, the presence of rare or non-native species in natural communities might result in negative relationships between biodiversity and ecosystem functioning (Dee et al. 2023). Moreover, changes in the performance of species under different environmental conditions can affect ecosystem functioning independently from changes in species richness (Ladouceur et al. 2022). Therefore, it remains debated how the findings of BEF experiments can be transferred to natural ecosystems (Dee et al. 2023; van der Plas 2019).

In natural ecosystems, environmental heterogeneity, such as spatial variation in climate and soil conditions, is expected to affect the relationship between biodiversity and ecosystem functioning (Gonzalez et al. 2020; Lemanski et al. 2022; Winfree et al. 2018). In such heterogeneous environments, the contribution 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, resulting in distinct species occurring in different environments (Gonzalez et al. 2020). Depending on the prevailing process, variation in species richness, species turnover, or both could drive the variation in ecosystem functioning (Albrecht et al. 2021).

Here, we assess to the extent to which environmental heterogeneity alters the effects of variation in species richness and species turnover on ecosystem functioning across various taxa and functions using the ecological Price equation (Figure 1; Albrecht et al. 2021; Bannar-Martin et al. 2018; Fox and Kerr 2012). In particular, we apply this approach to data on ecosystem functions of woody plants, frugivorous birds, ants and soil arthropods to study the contribution of variation in species richness and turnover to variation in ecosystem functioning along two tropical elevational gradients in the Ecuadorian Andes in south-eastern Ecuador and on Mt. Kilimanjaro in Tanzania. Both elevational gradients encompass multiple-ecosystem types (e.g., lower to upper montane forest) and cover a broad gradient of environmental conditions (e.g., climate, soil conditions, natural and disturbed ecosystems) and have distinct biogeographic histories and therefore also distinct species pools. Using these data, we test two main hypotheses: (i) The contribution of variation in species richness and turnover to variation in ecosystem functioning (i.e., the diversity effect) 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 more strongly driven by variation in species richness than by species turnover between communities (Albrecht et al. 2021).

## 2 | Material and Methods

### 2.1 | Study Sites

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 1000–3000 m a.s.l., including near-natural (thereafter called undisturbed) and human-modified (thereafter called disturbed) forest ecosystems. In both mountain regions, we assessed ecosystem functions and species richness on a common pool of sites, but not all functions could be measured on every study site.

Data for each function and taxon diversity were collected both in the Ecuadorian Andes and on Mt. Kilimanjaro. In Ecuador, sampling took place on 15 to 67 study sites (median = 18 study sites) in and next to Podocarpus National Park (PNP), with the central research station located in the valley of Rio San Francisco (Estación Científica San Francisco; Lat. 3°58′18″ S (−3.971667),

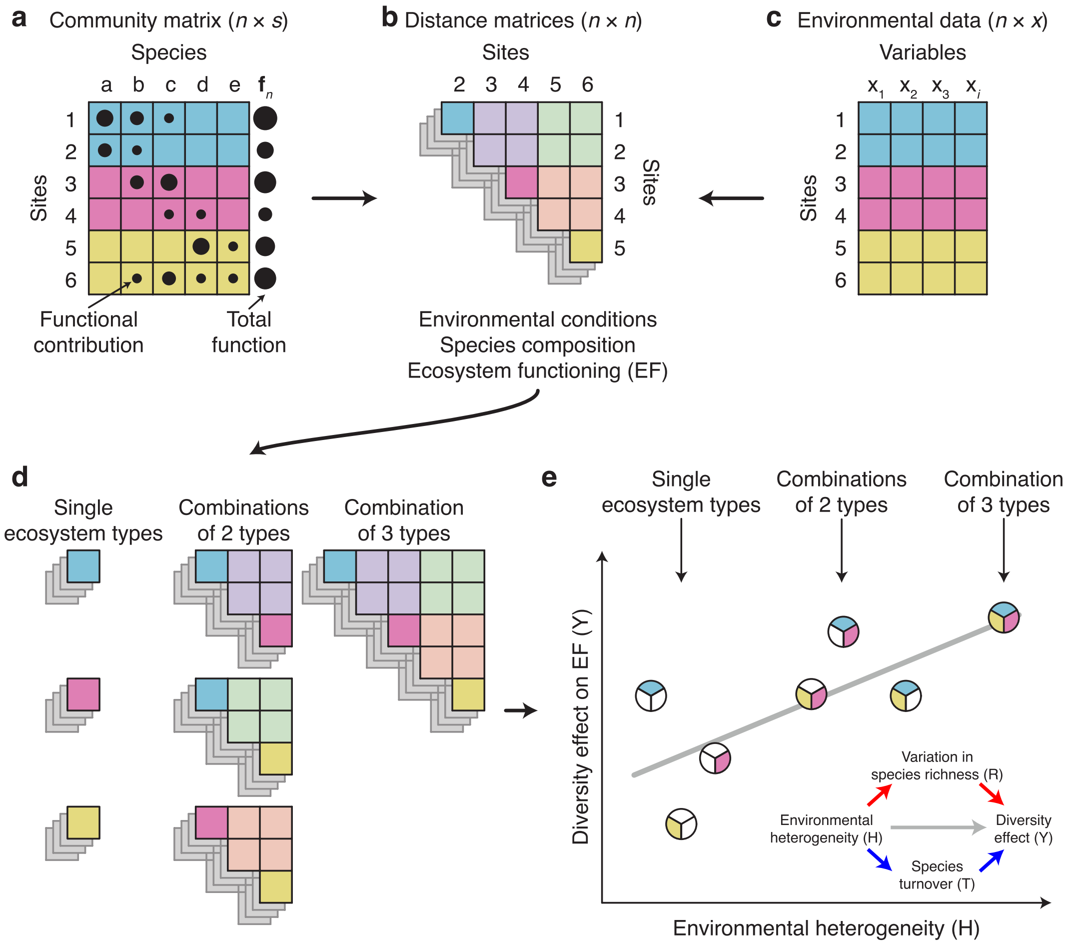

**FIGURE 1** | The applied analytical approach to investigate the effect of diversity on ecosystem functioning in heterogeneous environments. (a) A community matrix showing the contribution (filled circles) of each species to ecosystem functioning at six sites belonging to three different ecosystem types (*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 of each species. 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. Colours 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 for the comparison of the relative contribution of diversity due to variation in species richness and turnover to variation in ecosystem functioning between communities (i.e., the diversity effect) within and across ecosystem types. (e) The 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 colours). 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).

Long. 79°4′45″ W (−79.079167); Beck et al. 2019, Bendix et al. 2021). On Mt. Kilimanjaro, sampling was conducted on 12 to 30 study sites (median = 29 study sites) at the southern and southeastern slopes (Tanzania, East Africa; 2°45′–3°25′ S, 37°00′–37°43′ E; Peters et al. 2019; see Table S1.1 for more details on the number of study sites per function).

The climate in PNP in Ecuador is tropical humid, with mean annual temperatures ranging between 19°C and 13°C (Bendix et al. 2006; Richter 2003). The studied gradient at Mt. Kilimanjaro is wider in its thermal condition, with mean annual temperatures decreasing from 14°C–18°C at the lowlands to 8.8°C–10°C at 2770–3060 m a.s.l. (Peters et al. 2019). Precipitation in Ecuador ranges from approximately 2300 mm at 1850 m a.s.l. to more than 6000 mm at 3100 m a.s.l. (Bendix et al. 2006). On Mt. Kilimanjaro, rainfall peaks at ~2200 m a.s.l. with about 2700 mm annually (Hemp 2006a; Peters et al. 2019). Land-use history differs between the two regions. The Ecuadorian study sites are embedded in and around protected montane forest of PNP. Mt. Kilimanjaro's lowland ecosystems have long been shaped by fire, wood extraction, and agroforestry practices, leaving only the areas above 1800 m a.s.l. protected within the Kilimanjaro National Park (Hemp 2006a, 2006b; Peters et al. 2019).

The study sites encompassed three main elevational forest zones in both systems. Premontane forests (disturbed and undisturbed) were studied in Ecuador at 960–1268 m a.s.l. in the Bombuscaro area within and adjacent to PNP. On Mt. Kilimanjaro, the corresponding elevational belt was represented by lower montane forest and Chagga home gardens between 1171 and 2097 m a.s.l.

At the lower montane level, Ecuadorian sites (1850–2450 m a.s.l) were situated on the humid eastern slopes in the valley of the Rio San Francisco at the border of and next to the PNP (Reserva Biológica San Francisco). On Mt. Kilimanjaro, Ocotea forests (disturbed and undisturbed) were investigated between 2150 and 2741 m a.s.l. At the upper montane level, forests (disturbed and undisturbed) in Ecuador were studied at 2679–2931 m a.s.l. in the Cajanuma area within and adjacent to the PNP. On Mt. Kilimanjaro, we investigated Podocarpus forests (disturbed and undisturbed) at 2753–3009 m a.s.l. (see Table S1.2 for more details on the habitat types). In Ecuador, disturbed sites here were located on private land, mostly embedded in pastures and covered by bracken fern succession or exotic pine plantations (Curatola Fernández et al. 2015; Knoke et al. 2014, 2016). We included both disturbed and undisturbed ecosystem types in the analyses as previous work on Mt. Kilimanjaro indicated that the relationship between environmental heterogeneity and the diversity effect does not differ between disturbed and undisturbed ecosystem types (Albrecht et al. 2021).

## 2.2 | Environmental Variables

We characterised environmental heterogeneity by combining soil, mean annual air temperature and annual precipitation data (Appendix S1, Methods of 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 characterise soils, we used topsoil organic carbon content and C/N and N/P ratios. The ecosystem types and mountain systems showed strong variation in these environmental variables (Table S1.3).

## 2.3 | Ecosystem Functions

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). Biomass stocks were used as proxies for ecosystem functioning because they represent the accumulated outcome of various ecosystem processes (e.g., growth, energy storage and resource acquisition) and are indicators of ecosystem health and productivity (Loreau et al. 2021; O'Connor et al. 2017; D. Tilman 1997). For six of the seven functions, we had direct estimates of species-specific functional contributions in each community. For litter decomposition, we used site-level data on decomposition rates and allocated portions of the total ecosystem function proportional to the relative abundances of species in the community (following Garnier et al. 2004; Winfree et al. 2015). 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 from existing literature (for birds; Dunning 2008; Wilman et al. 2014) or morphometric measurements. For trees, we used basal area as a proxy for aboveground biomass (AGB) (Ensslin et al. 2015; Homeier and Leuschner 2021). More detailed information on the assessment of the specific biomass stocks is given in Appendix S1.

To measure the process rates of seed dispersal by birds, resource use by ants, and litter decomposition by microorganisms, process-specific protocols were used. In the Ecuadorian Andes and at Mt. Kilimanjaro, we calculated species-specific contributions to seed dispersal as the number of visits to all fruiting plants by each bird species (Quitián et al. 2018; Albrecht et al. 2018). To assess resource use by ants, bait experiments were conducted at each study site. To study net litter decomposition rates, standardised litter bags with leaves or roots were utilised in the Ecuadorian Andes (Marian et al. 2018) and litterbags filled with dried maize straw at Mt. Kilimanjaro (Peters et al. 2019). In both systems, 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. 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). More detailed information on the assessment of process rates is given in Appendix S1.

## 2.4 | Quantifying the Effects of Species Richness and Turnover on Ecosystem Functioning

Variation in ecosystem functioning between communities can arise from three proximate processes (Albrecht et al. 2021; Bannar-Martin et al. 2018; Fox and Kerr 2012): (1) variation in species richness due to species gains and losses, (2) species turnover due to changes in species identities or (3) a change in the functional contributions of species that are shared between communities (e.g., due to variation in abundance or individual performance; Figure 1). Here, we combine a variant of the ecological Price equation with the concept of β-diversity to quantify the relative contributions of these mechanisms to variation in ecosystem functioning (Albrecht et al. 2021). In brief, this approach is based on a community matrix **F** ($n \times s$) describing the contribution of $s$ species from a regional species pool to a given ecosystem function at $n$ study sites (communities hereafter; Figure 1). Based on matrix **F**, we first quantify the relative contribution of diversity due to the combined effects of variation in species richness and species turnover to the variation in ecosystem functioning between communities, which we term the diversity effect ($Y$; for details see Appendix S1). The metric ranges between zero and one, and it equals zero if all variation in ecosystem functioning between communities results from variation in the functional contributions of the same shared species between communities. Conversely, the metric equals one if all variation in ecosystem functioning arises from the combined effects of variation in species richness and species turnover. To further resolve whether the contribution of diversity to variation in ecosystem functioning between communities is driven by variation in species richness or species turnover, we partitioned the variation in species composition between communities (i.e., $\beta$-diversity) into variation due to differences in species richness (R) and due to species turnover (T) and related both components to the diversity effect (Albrecht et al. 2021; Legendre 2014). 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 Figure S1.1. Because our metric for the diversity effect is an absolute measure, we also quantified the correlations of the raw values of $\Delta f_i$ with $\Delta d_i$ and $\Delta_{si}$ to assess how strongly total variation in ecosystem functioning between communities ($\Delta f_i$) is related to variation in ecosystem functioning due to differences in species richness and turnover ($\Delta d_i$), and to variation in ecosystem functioning due to changes in the contributions of shared species ($\Delta s_i$; Figure S1.2). Across all 14 functions as well as for individual functions, we observed a strong positive correlation between $\Delta f_i$ and $\Delta d_i$ (Figure S1.2 and Table S1.4). Moreover, across the 14 ecosystem functions, the diversity effect was strongly positively related to the correlations between $\Delta f_i$ and $\Delta d_i$ of individual functions ($r=0.78$; Figure S1.2) and strongly negatively related to the correlation between $\Delta f_i$ and $\Delta s_i$ ($r=-0.89$; Figure S1.2). This indicates that our metric of the diversity effect is able to quantify the contribution of differences in species richness and turnover to the total variation in ecosystem functioning between communities. For more details on the analytical approach, see the Supporting Information.

## 2.5 | Quantifying Environmental Heterogeneity

We quantified environmental heterogeneity between communities using a distance-based approach. We used the Gower distance to determine the environmental distance between communities based on a set of environmental variables (temperature, precipitation, soil variables (N/P, C/N, organic C)). The Gower distance is preferred over the Euclidean distance as it is less sensitive to extreme values and facilitates the inclusion of categorical measures. To ensure comparability, we standardised all environmental variables by their ranges. The range standardisation ensures that each environmental variable contributes equally to the distance metric, and the maximum value of the distance function is 1. As some communities had missing data for some environmental variables, we calculated the pair-wise distances by using a pair-wise deletion of missing observations (for details see Appendix S1, Methods: Analytical approach).

## 2.6 | Assessing How Environmental Heterogeneity Influences the Diversity Effect

To evaluate how environmental heterogeneity directly impacts the diversity effect on ecosystem functioning and how variation in species richness and turnover mediates this effect, we analysed the relationships between environmental heterogeneity, variation in species richness, species turnover and the diversity effect within and across ecosystem types. To do so, we classified comparisons between pairs of sites into those within the same ecosystem type and those spanning multiple ecosystem types (Figure 1d). We then averaged these comparisons for different numbers and combinations of ecosystem types (ranging 1–6 ecosystem types) to obtain estimates of environmental heterogeneity, variation in species richness, species turnover and the diversity effect (Figure 1e).

## 2.7 | Statistical Analysis

To test our first hypothesis, we fitted a multiple-membership mixed-effects model (MMMEMs) (Park and Beretvas 2020) to the data from both mountain regions to assess the relationship between environmental heterogeneity and the diversity effect (Table S1.5). 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 and 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 S1.5). 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 (Figure 1e). To do so, we constructed three MMMEMs (sub-models hereafter) that described the implied causal structure of the SEM (Figure 1e; Table S1.6). 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 S1.7). 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 S1.7).

We also assessed the raw relationships between species richness and ecosystem functioning across ecosystem types (Figure S1.3). To do so, we fitted a single linear mixed-effects model (MEM) to the data from both mountain regions to analyse the relationship between species richness and ecosystem functioning (Table S1.8). 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 were 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 across the studied functions (Table S1.8). As before, we compared models with and without an interaction term between region and species richness based on BIC (Table S1.9). As the relationships did not differ between the two regions (Table S1.9), we report the results of the model without the interaction terms in the main text.

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 customised 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).

## 3 | Results

In line with our first hypothesis, the diversity effect increased with increasing environmental heterogeneity in both mountain regions (Figure 2), with an average increase of 1.1% in the diversity effect for a 1% increase in environmental heterogeneity ($\beta_{H \rightarrow Y} = 0.57\%–1.6\%$, 95% CI, $z = 4.4$, $p < 0.001$; Table S1.5). We found no support for differences in the diversity effect or in the increase of the diversity effect with environmental heterogeneity between the two mountain regions (Tables S1.5 and S1.6).

However, the diversity effect and its relationship with environmental heterogeneity varied among ecosystem functions

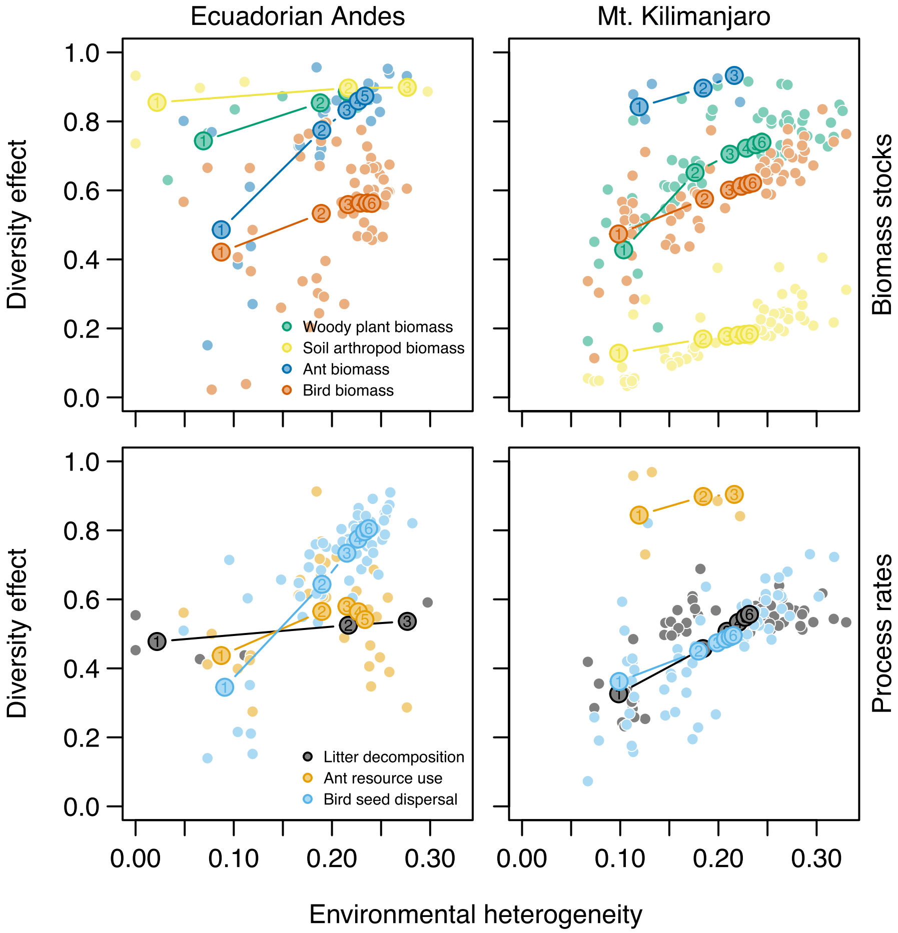

**FIGURE 2** | Relationship between environmental heterogeneity and the contribution of diversity to variation in ecosystem functioning. For two mountain regions, the relationship between environmental heterogeneity and the relative contribution of diversity due to variation in species richness and species turnover to the variation in ecosystem functioning (i.e., the diversity effect) 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. The number of combined ecosystem types is indicated within circles. The smaller light-coloured dots in the background depict the unaggregated raw pair-wise comparisons between communities. Sample sizes were: $N_{\text{pair-wise}}$ comparisons $= 533$, $n_{\text{ecosystem types}} = 12$, $n_{\text{functions}} = 14$.

(Figure 2). For instance, 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 (Figure 2). In contrast, the contribution of diversity to variation in ecosystem functioning was lowest for ant resource use and litter decomposition in the Ecuadorian Andes, and for soil arthropod biomass on Mt. Kilimanjaro (Figure 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 (Figure 2). We found almost no increase in the diversity effect with environmental heterogeneity for litter decomposition in the Ecuadorian Andes and for soil arthropod biomass on Mt. Kilimanjaro (Figure 2).

Across ecosystem functions and mountain regions, variation in species richness and turnover, on average, increased the contribution of diversity to variation in ecosystem functioning at similar magnitudes ($\beta_{R\to Y}=0.86$ [0.14–1.5, 95% CI], $z=2.5$, $p=0.013$; $\beta_{T\to Y}=1.0$ [0.56–1.5, 95% CI], $z=4.9$, $p<0.001$; Tables S1.10 and S1.11). We found no support for differences in these relationships between the two mountain regions (Table S1.11), but the effects of variation in species richness and turnover on the contribution of diversity to variation in ecosystem functioning varied among ecosystem functions (Figure 3). For example, the diversity effect on biomass stocks of birds was positively related to variation in species richness on Mt. Kilimanjaro, but negatively in the Ecuadorian Andes (Figure 3, Table S1.10). 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; Figure 3, Table S1.10).

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 (Figure 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 ($\beta_{H\to R}=0.64$ [0.26 to 1.0, 95% CI], $z=3.4$, $p<0.001$), but not by species turnover ($\beta_{H\to T}=0.10$ [−0.26 to 0.45, 95% CI], $z=0.59$, $p=0.56$; Figure 4; Table S1.11). Environmental heterogeneity did not directly increase the diversity effect ($\beta_{H\to Y}=0.20$ [−0.37 to 0.74, 95% CI], $z=0.72$, $p=0.47$), indicating that the effect of environmental heterogeneity on ecosystem functioning was primarily driven by increasing differences in species richness between communities as environmental heterogeneity increased. We found no support for differences in these relationships between the two mountain regions (Table S1.11).

We found a general increase in the magnitude of ecosystem functioning with increasing species richness on both

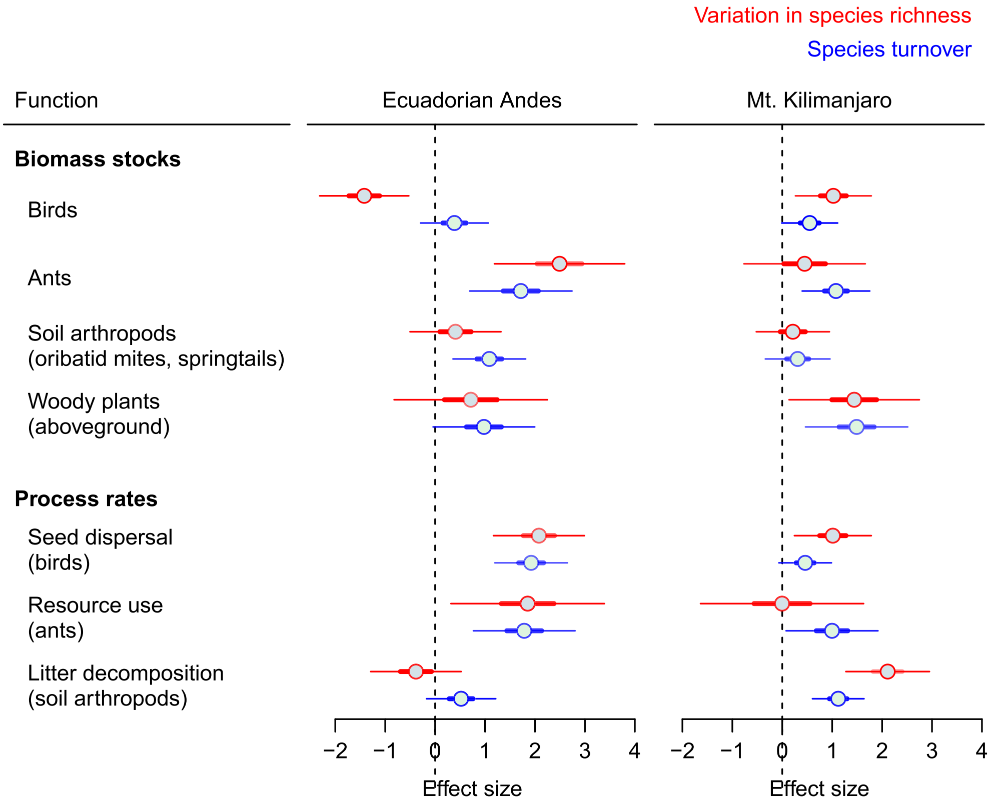

**FIGURE 3** | Estimated effects of variation in species richness and species turnover on the contribution of diversity to variation in ecosystem functioning for individual ecosystem functions. Shown are random effect estimates (circles), as well as 50% and 95% Confidence Intervals (Cis, thick and thin lines, respectively) based on the MMMEMs for the effects of variation in species richness (red) and species turnover (blue) on the diversity effect (Table S1.10). The effect sizes reflect the expected change in the diversity effect for a 1% change in the predictor variable (e.g., 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: $N_{\text{observations}}=533$, $n_{\text{ecosystem types}}=12$, $n_{\text{functions}}=14$.

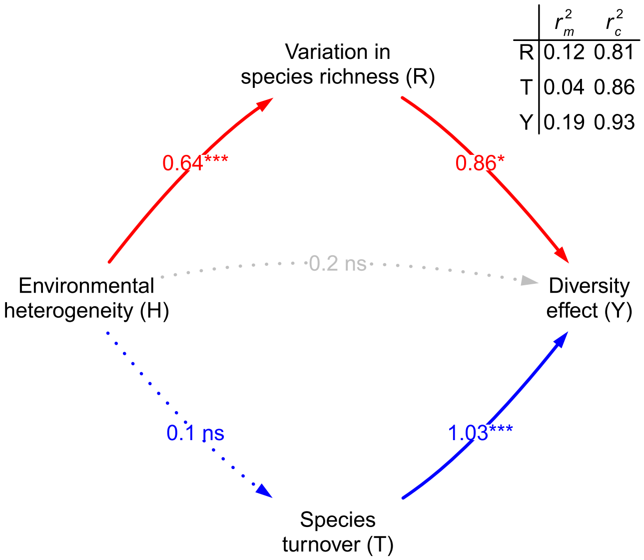

**FIGURE 4** | Structural equation model quantifying the direct effect of environmental heterogeneity (H) on the contribution of diversity to variation in ecosystem functioning (i.e., the diversity effect, Y), as well as the indirect effects mediated by variation in species richness (R) and species turnover (T; Table S1.11). The effect sizes reflect the expected change in the response variable for a 1% change in the predictor variable (e.g., 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 lines and ns indicate non-significant effects ($p > 0.05$). $R^2_m$, marginal $R^2$ 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. Models are based on data from the Ecuadorian Andes and from Mt. Kilimanjaro in Tanzania. Sample sizes were: $N_{\text{observations}} = 533$, $n_{\text{ecosystem types}} = 12$, $n_{\text{functions}} = 14$.

mountains (slope: 1.1 [0.46 to 1.7, 95% CI], $z = 3.6$, $p < 0.001$; $R^2_m = 0.25$; Table S1.8). Model selection indicated that the slope of this relationship did not differ between the two mountain regions (Table S1.9). 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 (Figure S1.3).

## 4 | Discussion

Here, we quantified the contribution of diversity due to variation in species richness and turnover to variation in ecosystem functioning between communities along two tropical elevational gradients. We showed that the contribution of diversity to variation in ecosystem functioning increased with increasing environmental heterogeneity along both elevational gradients. Moreover, we found that both variation in species richness and turnover contributed to the diversity effect on ecosystem functioning. However, the increase in the diversity effect with environmental heterogeneity was solely mediated by variation in species richness between communities because species turnover was unrelated to environmental heterogeneity in our study systems. These patterns were consistent in both mountain regions.

### 4.1 | The Diversity Effect Increases With Environmental Heterogeneity

We observed an increase in the diversity effect with increasing environmental heterogeneity on both mountains (Figure 2), reinforcing findings from previous studies (e.g., Albrecht et al. 2021; Martinez-Almoyna et al. 2019). This suggests that the role of species richness and turnover in driving ecosystem functioning relative to changes in the abundance or performance of dominant species becomes more important as environmental heterogeneity increases. The importance of changes in species abundance for variation in ecosystem functioning between communities in homogeneous environments (i.e., within the same ecosystem type) mirrors previous findings from insect-pollinated crop systems where changes in the contribution of abundant species were the main driver of spatiotemporal variation in crop pollination services (Winfree et al. 2015). Our findings are also in line with the observations from experiments that ecosystem functioning in a single year and site is often driven by a few dominant species that exploit the available resources most efficiently (Allan et al. 2011; Isbell et al. 2011, 2018). Overall, our results suggest that dominant species play a larger role in driving ecosystem functioning when community dynamics are more strongly shaped by stochastic fluctuations in species abundances than by environmental filtering, such as along narrow environmental gradients.

Our results also indicate that species complementarity may amplify the diversity effect at larger scales and under increasing environmental heterogeneity. In heterogeneous environments, a greater variety of microhabitats and resource conditions promotes niche differentiation among species (Brown et al. 2013; David Tilman 1999), enabling species to coexist and functionally complement each other in different communities. Additionally, stronger species sorting and dispersal limitation can reinforce the specialisation of species to specific habitat conditions, leading to greater differentiation in functional roles and enhancing the contribution of changes in species richness and turnover to variation in ecosystem functioning along broad environmental gradients (Hooper et al. 2005).

Although the diversity effect on average increased with environmental heterogeneity across both mountain regions, its strength varied across functions (Figure 2). The observed variation in biodiversity–ecosystem function relationships across functions and mountain regions shows that it can be difficult to generalise from one function to another. While some functions such as seed dispersal by birds and ant biomass showed stronger diversity effects in the Andes, others like decomposition and ant resource use responded more strongly in Kilimanjaro, illustrating that different taxa and types of functions may be shaped by distinct environmental filters and biogeographic histories. These divergent patterns likely reflect differences in the prevalence of community assembly mechanisms among taxa and contexts. Our study design does not allow for a mechanistic dissection of these taxon- and function-specific responses, but future studies could systematically compare multiple functions across diverse taxonomic groups and tropical and temperate systems.

### 4.2 | Effects of Variation in Species Richness and Species Turnover on the Diversity Effect Varies for Individual Ecosystem Functions

In both mountain regions, we found that the different contributions of diversity to ecosystem functioning can be attributed to both changes in species richness and turnover. This suggests that two non-exclusive processes likely drove the diversity effect. 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 the performance of species under particular environmental conditions determines differences in ecosystem functioning.

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 favourable 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, in turn affecting ecosystem functioning (Grace et al. 2016). Our findings suggest that both species sorting and species coexistence are driving variation in species richness along the two elevational gradients; however, the relative importance of these factors can vary depending on the type of ecosystem function.

Our results indicate that the relative effect of species richness and species turnover on ecosystem functioning varies across different functions. This variation complicates generalisations about how biodiversity supports ecosystem functioning. For example, the negative relationships of biomass stocks of birds and decomposition by soil arthropods to the variation in species richness in the Ecuadorian Andes compared to Mt. Kilimanjaro (Figure 3) suggest that the relationship between species richness and ecosystem function can be context-dependent. For bird biomass, the negative relationship in the Andes (Figure 3) might reflect a scenario where high species richness leads to increased competition or resource partitioning, which could reduce biomass stocks. Additionally, the long evolutionary history and high species diversity of the Andean bird community (Jetz et al. 2012; Rahbek and Graves 2001) may result in greater functional redundancy, meaning that species turnover rather than richness plays a stronger role in maintaining biomass. In contrast, on Kilimanjaro, which is more geologically recent and biogeographically isolated (Hemp and Hemp 2018; Nonnotte et al. 2008), higher species richness might enhance biomass through complementary resource use or reduced competition, suggesting that species play more distinct functional roles in these communities. Overall, these examples highlight the complexity of biodiversity–ecosystem function relationships and the importance of considering biogeographical differences and the specific ecological context when assessing the relationship between species richness and ecosystem functions.

### 4.3 | The Increase in the Diversity Effect With Environmental Heterogeneity Was Driven Solely by Species Richness

We found that the increasing contribution of diversity to variation in ecosystem functioning with environmental heterogeneity was mainly driven by increasing variation in species richness. 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 and 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 in both 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). Previous studies of plant and bird communities in the Andes and on Mt. Kilimanjaro have also shown that environmental heterogeneity is related to abundance and richness differences of plants and birds within and between elevations (Barczyk et al. 2023; Ferger et al. 2017). The overall strong contribution of variation in species to the diversity effect along the two elevational gradients suggests that assembly processes related to species coexistence play a more prominent role in driving ecosystem functioning along tropical elevational gradients.

### 4.4 | Study Limitations

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 is 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 regions, 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. Such studies could also test the impact of specific environmental drivers, such as soil productivity, on ecosystem functioning.

## 5 | Conclusion

Our study demonstrates that the diversity effect on ecosystem functioning is mediated by environmental heterogeneity, with differences in species richness being the primary driver of this relationship. Despite the distinct biogeographical and evolutionary histories of the Ecuadorian Andes and Mt. Kilimanjaro, we observed consistent patterns in biodiversity–ecosystem functioning relationships, reinforcing the role of species coexistence as a key driver of ecosystem functioning in natural ecosystems. As biodiversity and ecosystem function data become increasingly available for more taxa and ecosystems, future large-scale analyses may provide deeper insights into the underlying mechanisms shaping variation in specific biodiversity–ecosystem functioning relationships in real-world ecosystems, which will be essential to support more effective conservation and management strategies.

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### Author Contributions

N.F., M.S., E.L.N., R.B., J.A. and A.W. conceptualised 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. and 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. and 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. conceptualised and supervised the data collection; J.A. and A.W. developed the analytical tools; J.A. analysed and visualised the data. All other authors commented on the manuscript and gave final approval for publication.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

The data and code to reproduce the analyses have been uploaded on Dryad at doi: https://doi.org/10.5061/dryad.fqz612k2j. If the dataset has been approved for publication by a member of our curation team, it will be made public. The link for peer review can be found under: http://datadryad.org/stash/share/lrK_jswM6RLY_pNuf7K8s9Jt4wj9dvUMYTksJ_4uq8o.

### Peer Review

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.70093.

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** Supporting Information. **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). **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). **Table S1:3:** Average (mean), standard deviation (SD), minimum values (min) and maximum values (max) of environmental variables (elevation, soil organic carbon, mean annual temperature, annual precipitation, soil C:N ratio and soil N:P ratio) for each habitat and mountain region. Units for elevation = m a.s.l.; soil organic carbon = Mg/ha; mean annual temperature = °C; annual precipitation = mm/year; soil C:N ratio = ration; Soil N:P ratio = ratio. **Table S1:4:** Correlation coefficients for the relationships between $\Delta F_i$ and $\Delta D_i$, as well as for relationships between $\Delta F_i$ and $\Delta S_i$, for individual functions in the two mountain regions (Andes, Ecuador and Mt. Kilimanjaro, Tanzania). $\Delta F_i$ = mean difference in the magnitude of a given ecosystem function between community *i* and all other communities; $\Delta D_i$ = mean difference in the magnitude of a given ecosystem function between community *i* and all other communities due to differences in species richness and species turnover; $\Delta S_i$ = mean difference in function between community *i* and all other communities due differences in the functional contributions of shared species. **Table S1:5:** 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 (Table S1.6). Sample sizes were: $n_{\text{observations}} = 533$, $n_{\text{ecosystem types}} = 12$, $n_{\text{functions}} = 14$. $Y$ = Diversity effect. $R^2_{\text{m}}$ = Marginal $R^2$ considering only the variance of the fixed effects (without the random effects). $R^2_{\text{c}}$ = conditional $R^2$ considering both the fixed and random effects. **Table S1:6:** 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. **Table S1:7:** 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. **Table S1:8:** 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 standardising 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: $n_{\text{observations}} = 353$, $n_{\text{site}} = 143$, $n_{\text{function id}} = 14$. $R^2{}_{\text{m}}$ = Marginal $R^2$ considering only the variance of the fixed effects (without the random effects). $R^2{}_{\text{c}}$ = *conditional* $R^2$ considering both the fixed and random effects. **Table S1:9:** 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 standardised and log-transformed species richness (log(S)), as well as a model including Region, log(S), and their interaction. **Table S1:10:** Summary of effect sizes for individual functions in both mountain regions based on the MMMEMs. Estimates of effect sizes are provided for the effects of (1) environmental heterogeneity on variation in species richness ($\beta_{\text{H}\rightarrow\text{R}}$), (2) environmental heterogeneity on species turnover ($\beta_{\text{H}\rightarrow\text{T}}$), (3) environmental heterogeneity on the diversity effect ($\beta_{\text{H}\rightarrow\text{T}}$), (4) variation in species richness on the diversity effect ($\beta_{\text{R}\rightarrow\text{Y}}$), and (5) variation in species turnover on the diversity effect ($\beta_{\text{T}\rightarrow\text{Y}}$). Shown are model estimates of the random slopes components from MMMEMs along with their standard error (SE) and $p$-values. Effect sizes that are significantly different from zero at $\alpha = 0.05$ are highlighted on boldface type. Note that the effect sizes for (4) $\beta_{\text{R}\rightarrow\text{Y}}$ and (5) $\beta_{\text{T}\rightarrow\text{Y}}$ are also shown in Figure 3 in the main text. The last row of the table shows the global model estimate of the effect sizes. **Table S1:11:** 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. 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. $R^2{}_{\text{m}}$, Marginal $R^2$ considering only the variance explained by the fixed effects. $R^2{}_{\text{m}}$, *conditional* $R^2$ considering the variance explained by both the fixed and random effects. **Figure S1:1:** Example scenarios of differences in ecosystem functioning between communities. (a) The matrix F ($n \times s$) 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. **Figure S1:2:** (a, b) Relationship of average total difference in the magnitude of a given ecosystem function between community $i$ and all other communities ($\Delta F_i$) with (a) average difference in ecosystem functioning due to changes in species richness and species turnover ($\Delta D_i$) and (b) with average difference in ecosystem functioning due to changes the functional contributions of shared species ($\Delta S_i$). The colours indicate different ecosystem functions. (c, d) Relationships of the diversity effect with (c) the strength of the correlation between $\Delta F_i$ and $\Delta D_i$ and (d) between $\Delta F_i$ and $\Delta S_i$ across the seven ecosystem functions and the two elevational gradients ($n = 14$). **Figure S1:3:** 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 standardising the values of ecosystem functions and species richness for each function by their mean values for a given function (i.e., $S'_i = \log(S_i/\text{mean}(S_i))$ and $F'_i = \log(F_i/\text{mean}(F_i))$). 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). Grey 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.

## Biographies

**Annemarie Wurz** obtained her PhD in Agroecology at the University of Goettingen, Germany, studying the effects of land use on biodiversity and ecosystem services in Madagascar. She is currently a postdoctoral researcher predicting changes in ecosystem functioning under climate and land-use change in Ecuador. The Conservation Ecology group led by Prof. Nina Farwig focuses on the effects of anthropogenic land use on biodiversity and ecological processes with the ultimate aim to developing sustainable use concepts.

**Jörg Albrecht** did his PhD in Conservation Ecology at the University of Marburg, Germany, investigating natural and human-induced dynamics in plant–animal networks in Poland. Now he is a postdoctoral researcher at the Senckenberg Biodiversity and Climate Research Centre studying global change effects on species interaction networks and ecosystem functions. The Functional Ecology and Global Change group led by PD Matthias Schleuning focuses on studying species interactions along anthropogenic gradients and large spatial scales.