ARTICLES
https://doi.org/10.1038/s41559-021-01550-9

nature ecology & evolution

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Species richness is more important for ecosystem functioning than species turnover along an elevational gradient

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Many experiments have shown that biodiversity enhances ecosystem functioning. However, we have little understanding of how environmental heterogeneity shapes the effect of diversity on ecosystem functioning and to what extent this diversity effect is mediated by variation in species richness or species turnover. This knowledge is crucial to scaling up the results of experiments from local to regional scales. Here we quantify the diversity effect and its components—that is, the contributions of variation in species richness and species turnover—for 22 ecosystem functions of microorganisms, plants and animals across 13 major ecosystem types on Mt Kilimanjaro, Tanzania. Environmental heterogeneity across ecosystem types on average increased the diversity effect from explaining 49% to 72% of the variation in ecosystem functions. In contrast to our expectation, the diversity effect was more strongly mediated by variation in species richness than by species turnover. Our findings reveal that environmental heterogeneity strengthens the relationship between biodiversity and ecosystem functioning and that species richness is a stronger driver of ecosystem functioning than species turnover. Based on a broad range of taxa and ecosystem functions in a non-experimental system, these results are in line with predictions from biodiversity experiments and emphasize that conserving biodiversity is essential for maintaining ecosystem functioning.

Over the past few decades, hundreds of biodiversity experiments have accumulated evidence that species richness enhances ecosystem functioning[1–3]. However, it remains uncertain to what extent these effects are relevant in naturally assembled communities and at large spatial scales[4–7]. This uncertainty stems from the fact that, unlike real ecological communities, experimental communities are established in homogeneous environments at small spatial scales to minimize the influence of confounding factors[6]; they are typically assembled randomly to isolate the effects of species richness from those of species identity[7–15]; and experiments allow processes that operate within communities (for example, local niche partitioning and competition)[16] but eliminate processes that operate between communities (that is, metacommunity assembly processes, such as species sorting or dispersal)[14,15]. It therefore remains unknown how community assembly processes alter the relationship between biodiversity and ecosystem functioning in heterogeneous environments[4–6], and which aspects of diversity shape ecosystem functioning in naturally assembled communities. This has limited the transfer of the results of biodiversity experiments from local to regional scales, which are most relevant to management and conservation[4,6].

Environmental heterogeneity (that is, the spatial or temporal variability in local environmental conditions) plays a critical role in community assembly processes[5,6,17–19]. On the one hand, local environmental conditions set upper limits to the number of species that can coexist locally[20,21]. Environmental heterogeneity may therefore increase the variation in species richness between localities if it increases the variation between localities in those environmental factors that limit local species coexistence. On the other hand, environmental heterogeneity may increase species turnover, because species differ in their niche requirements so that different species thrive in different environments (sensu 'species sorting' in metacommunity theory)[6,18]. Across broad environmental gradients, the effects of species sorting on species turnover are expected to increase more strongly than variation in factors that limit local species coexistence[6]. Variation in ecosystem functioning in heterogeneous environments might therefore be more strongly driven by species turnover than by variation in species richness. Yet,

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disentangling the effects of variation in species richness and species turnover on ecosystem functioning in naturally assembled communities represents a methodological challenge[7,13,14], because there is a lack of analytical frameworks capable of dealing with complete species turnover across broad environmental gradients.

To fill this gap, we introduce a framework to study the contributions of these aspects of diversity to variation in ecosystem functioning in non-experimental settings. In particular, our framework allows us to quantify the variation in ecosystem functioning resulting from variation in species richness and species turnover (the two fundamental components of β-diversity; Fig. 1)[22,23]. We use this framework to assess to what extent environmental heterogeneity alters the effects of variation in species richness and species turnover on ecosystem functioning across various taxa and functions. First, we test whether the diversity effect (that is, the combined effects of variation in species richness and species turnover on ecosystem functioning) is related to environmental heterogeneity. Second, we test whether the diversity effect is primarily mediated by variation in species richness or by species turnover. We hypothesize that (1) the effect of diversity on ecosystem functioning increases with environmental heterogeneity[6,20,24,25] and that (2) this increase is driven by increased species turnover rather than by variation in species richness in heterogeneous environments[5,6,26–28].

Results

Quantifying the effect of diversity on ecosystem functioning. Our framework can be applied to any ecosystem function comprising the summed functional contributions of individual species (Fig. 1), which is the case for standing biomass stocks and most ecosystem processes[1] (but see Bell et al.[29]). The framework builds on the assumption that variation in ecosystem functioning between communities can arise from three proximate mechanisms: (1) variation in species richness, (2) species turnover 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; Fig. 1). We combine a variant of the Price equation from evolutionary biology[14,30] with the concept of β-diversity[22,23] to quantify the relative contributions of these mechanisms to variation in ecosystem functioning (Methods). Notably, our framework generalizes previous approaches[14,30], as it can be applied to any pair of communities regardless of whether they have species in common, so that the contribution of diversity to variation in ecosystem functioning can be quantified across broad environmental gradients with complete species turnover.

The framework 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 (hereafter referred to as communities; Fig. 1). This requires the contribution of each species to a given ecosystem function (for example, biomass stocks or process rates) to be known or approximated from data on species' relative abundances. On the basis of matrix **F**, we first quantify the relative contribution of diversity due to variation in species richness and species turnover to the variation in ecosystem functioning between communities (hereafter, the diversity effect). 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 (Fig. 1c). Conversely, the metric equals one if all variation in ecosystem functioning arises from the combined effects of variation in species richness and species turnover (Fig. 1a,b). To disentangle whether the diversity effect is driven by variation in species richness or species turnover, we partition the variation in species composition between communities (that is, β-diversity) into variation due to differences in species richness and species turnover and relate both components to the diversity effect (Methods)[22,23].

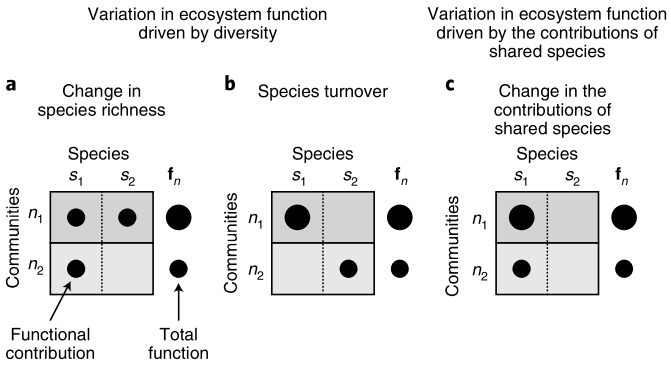

Fig. 1 | Quantifying the effect of diversity on ecosystem functioning. **a–c**, Illustration of the three proximate mechanisms underlying variation in ecosystem functioning between communities. Variation in the level of ecosystem functioning between two communities may arise due to variation in species richness (**a**), species turnover (**b**) or changes in the functional contributions of those species that are shared between communities (for example, due to variation in abundance or individual performance) (**c**). In each case, the matrix **F** ($n \times s$) describes the functional contribution of s species (here s_1 and s_2) to ecosystem functioning ($\mathbf{f}_n$) in n communities (here n_1 and n_2). The approach therefore requires that the ecosystem function of interest comprises the summed functional contributions of individual species. Circle size depicts the magnitude of species' functional contributions to ecosystem functioning in each community.

Application to naturally assembled communities. We applied this framework to a set of 22 ecosystem functions controlled by microorganisms, plants and animals. Fourteen of these functions were related to biomass stocks of diverse taxa, and eight functions were related to process rates such as pollination, brood parasitism or litter decomposition (Fig. 2a,b). For all of these functions, we quantified species-specific contributions to ecosystem functioning at up to 60 study sites that were distributed across 13 ecosystem types along a broad 3.7 km elevational gradient (850–4,550 m above sea level (a.s.l.)) on the southern slopes of Mt Kilimanjaro, Tanzania (Extended Data Figs. 1 and 2; Methods)[31,32]. For 5 of the 22 functions without direct estimates of species-specific functional contributions, we approximated species-specific contributions in each community on the basis of relative abundances (or biomass) of the species (Methods). For these functions, we therefore assumed that the functional contribution of a species in a given community was proportional to its relative abundance (or biomass)[33,34]. Importantly, all of the 22 functions were positively related to species richness, and this relationship was significant in 19 of the 22 functions (explained variation across functions: $r^2 = 0.42 \pm 0.23$ (mean ± s.d.), range = 0.01–0.75; Extended Data Fig. 3).

To test our initial hypotheses, we quantified for each function the contribution of diversity to variation in ecosystem functioning on the basis of comparisons between communities within the same ecosystem type and contrasted this with comparisons across ecosystem types. This means that we compared the diversity effect between short (within ecosystem types) and long environmental gradients (across ecosystem types). This resulted in 43 estimates of the diversity effect across the 22 functions ($n = 21$ within and $n = 22$ across ecosystem types; Fig. 2a,b and Extended Data Fig. 4). In addition, we quantified environmental heterogeneity within and across ecosystem types as the average environmental distance between study sites on the basis of a combination of 11 variables related to climatic conditions (mean annual temperature, mean annual precipitation and relative humidity), land use (biomass removal, agricultural inputs and landscape composition) and soil properties

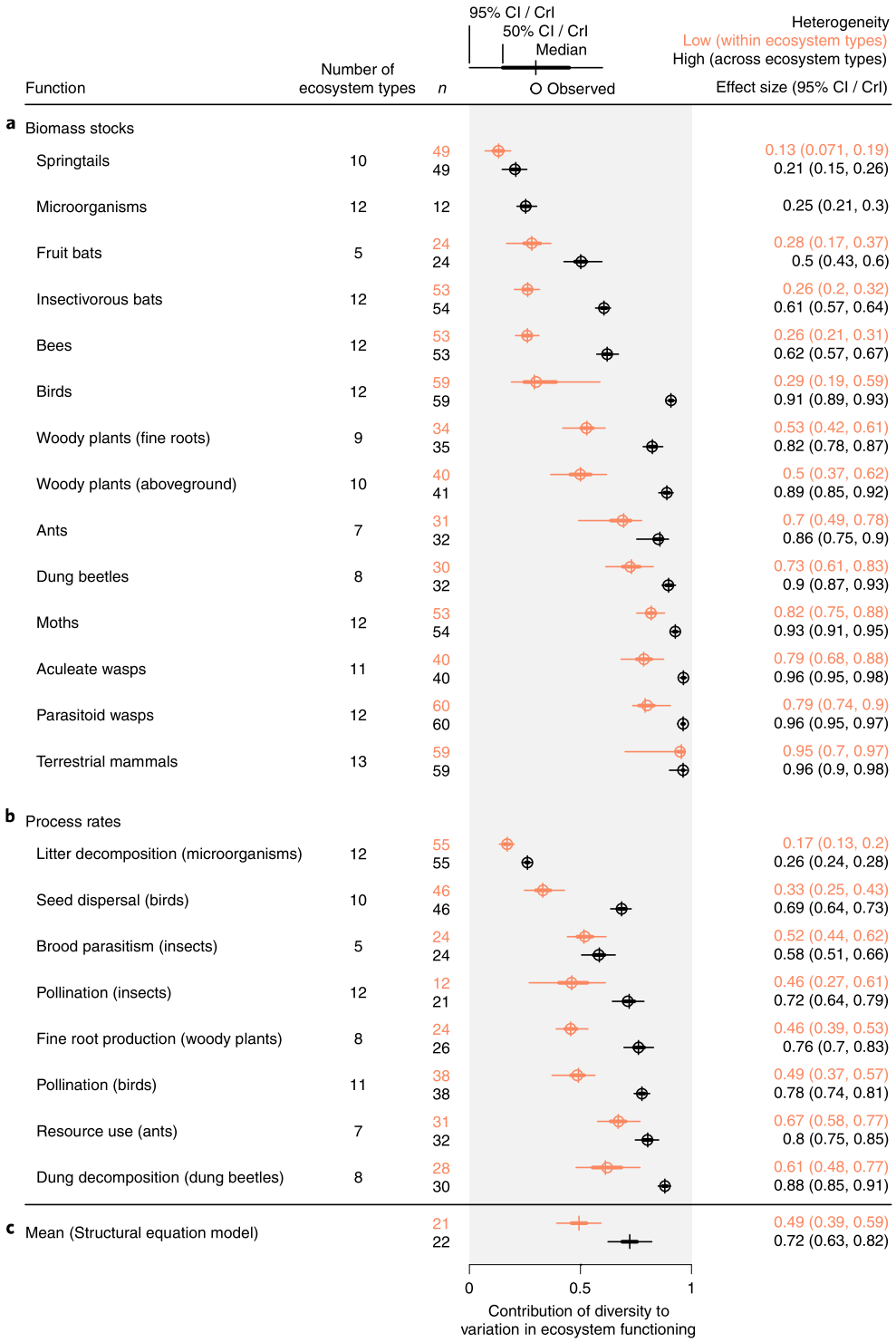

Fig. 2 | Effect of diversity on ecosystem functioning within and across ecosystem types. a,**b**, Diversity effects within and across ecosystem types are based on 14 functions related to biomass stocks (**a**) and 8 functions related to rates of ecosystem processes (**b**). In **a** and **b**, the medians and 50% and 95% confidence intervals (CIs) of the effect sizes are based on bootstrap subsampling without replacement (Methods). The observed estimates are based on the full sample of study sites. The sample sizes (*n*) in **a** and **b** indicate the number of study sites on which the estimates of the diversity effect were based. In **a** and **b**, ecosystem functions are ordered by the magnitude of the diversity effect (smallest to largest). **c**, The diversity effects for comparisons within and across ecosystem types as estimated by the Bayesian hierarchical structural equation model are given (medians and 50% and 95% credible intervals (CrIs); see Methods for details). The sample sizes in **c** indicate the number of effect sizes within and across ecosystem types, respectively. The diversity effect ranges between 0 (all variation in ecosystem functioning arises from variation in the functional contributions of the same shared species) and 1 (all variation in ecosystem functioning arises from variation in species richness and species turnover). Note that the within-ecosystem comparison for biomass stocks of microorganisms is missing because data were available for only one replicate per ecosystem type.

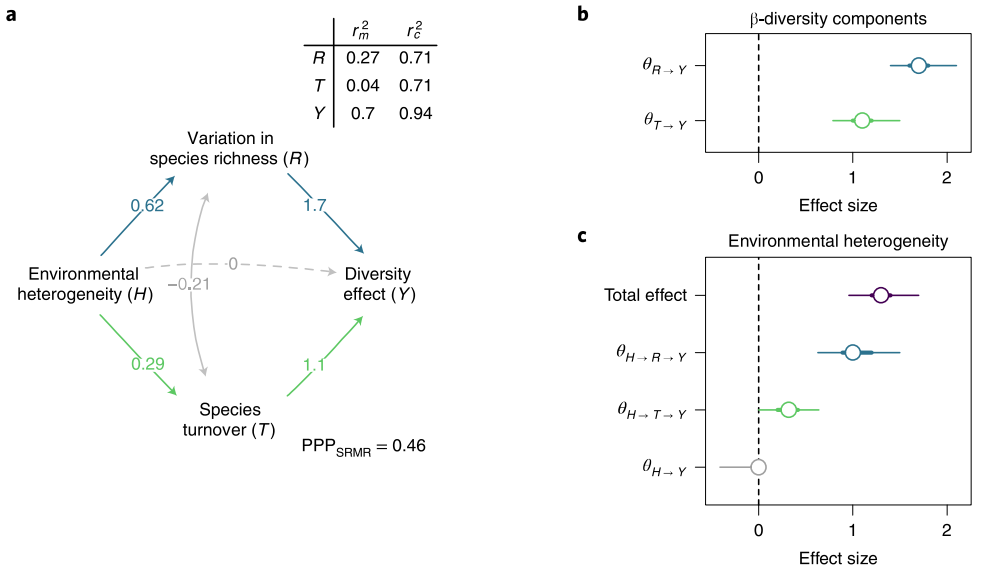

Fig. 3 | Environmental heterogeneity controls the effect of diversity on ecosystem functioning. a, Topology of the Bayesian hierarchical structural equation model with the strongest support. The figure shows the direct effects of environmental heterogeneity (*H*) on the contribution of diversity to variation in ecosystem functioning (that is, the diversity effect, *Y*) and the indirect effects that were mediated by variation in species richness (*R*) and species turnover (*T*). The solid paths were supported by the Bayesian variable selection, whereas the dotted path was not (Table 1 and Extended Data Fig. 7). The grey double-headed arrow depicts a covariance term that accounts for correlated errors due to common unmeasured sources of variance. The explained variance for each endogenous variable is denoted by r_m^2 (marginal variance explained by fixed effects) and r_c^2 (conditional variance explained by fixed and random effects). Posterior predictive *P* values based on standardized root mean square residuals (PPP$_{SRMR}$) close to 0.5 indicate close fit of the model to the covariance structure of the data. **b**, Estimated effects of variation in species richness and species turnover on the contribution of diversity to variation in ecosystem functioning. **c**, Estimated total effect size (purple) of environmental heterogeneity, as well as the direct (grey) and indirect species-richness-mediated and turnover-mediated effects (blue and green, respectively). The effect sizes (θ) reflect the expected change in the response variable for a 1% change in the predictor variable (for example, $\theta_{R\to Y}=1.7$ means that an increase of 10% in variation in species richness causes an increase of 17% in the diversity effect). The data in **b** and **c** are medians (circles), as well as 50% and 95% CrIs based on the posterior distribution of the estimated model parameters (thick and thin lines, respectively). The sample size is $n=43$ diversity effects ($n=21$ within and $n=22$ across ecosystem types, respectively).

(organic carbon, pH, C/N ratio, N/P ratio and available water capacity; Methods). Environmental heterogeneity in terms of the selected variables increased with the number of ecosystem types ($r^2=0.98$; Extended Data Fig. 5) and was on average 2.6 ± 0.44 (mean ± s.d.) times higher across than within ecosystem types (Extended Data Fig. 6a). To quantify the effect of environmental heterogeneity on the contribution of diversity to variation in ecosystem functioning, we used a Bayesian hierarchical structural equation model with a stochastic variable selection procedure (Fig. 3a, Extended Data Fig. 7 and Methods). This model allowed us to quantify the direct effect of environmental heterogeneity, as well as the indirect effects that were mediated by variation in species richness and species turnover (Table 1 and Fig. 3b,c).

Consistent with our first hypothesis, the model revealed that the effect of diversity on ecosystem functioning increased from 49% to 72% as environmental heterogeneity increased (2ln(Bayes factor) = 14 (hereafter 2lnBF), decisive support; Table 1 and Fig. 2c). This indicates that increasing environmental heterogeneity by considering multiple instead of single ecosystem types increased the contribution of diversity to variation in ecosystem functioning and decreased the effects of variation in the functional contributions of the same shared species between communities. The model further revealed that the contribution of diversity to variation in ecosystem functioning was strongly related to both variation in species richness and species turnover (Table 1, Fig. 3b and Extended Data Fig. 8). However, in contrast to our second hypothesis, the effect of variation in species richness was stronger than the effect of species turnover (effect size comparison: $\theta_{R\to Y}>\theta_{T\to Y}$, 2lnBF = 11, decisive support; Table 1 and Fig. 3b). In addition, the increase in the diversity effect with environmental heterogeneity was almost exclusively mediated by variation in species richness, whereas species turnover was of minor importance (effect size comparison: $\theta_{H\to R\to Y}>\theta_{H\to T\to Y}$, 2lnBF = 8.5, strong support; Table 1 and Fig. 3c). The fact that ecosystem functioning was more strongly related to variation in species richness than to species turnover is remarkable because species turnover along the elevational gradient was consistently larger than variation in species richness across the 22 ecosystem functions (average species turnover of 47% versus average variation in species richness of 38%; paired *t*-test: $t=2.85$, $n=22$, $P<0.01$; Extended Data Fig. 4).

These results were robust to the exclusion of those functions (5 out of 22) for which we had only indirect estimates of species-specific contributions to ecosystem functioning (Extended Data Fig. 9). The results also remained unaffected when we excluded study sites with disproportionately low or high levels of ecosystem functioning (Extended Data Fig. 9) and when we analysed the data from natural and anthropogenic ecosystem types separately (Extended Data Fig. 9). Finally, we also assessed to what extent our conclusions were affected by the potentially confounding effects of variation in environmental factors along the elevational gradient (for example, climatic conditions or soil properties). To do so, we calculated the diversity effect sizes on the basis of the residuals from the linear or nonlinear elevational trends in the ecosystem functions (deviance explained by elevation across functions: $r^2_{dev}=0.33\pm0.21$ (mean ± s.d.), range = 0.05–0.77; Extended Data Fig. 10 and Methods). Accounting for elevational trends in ecosystem functioning only reduced the average contribution of diversity to variation in ecosystem functioning across ecosystem types from 72% to 69%

(paired t-test: $t = -2.45$, $n = 22$, $P = 0.023$). Importantly, our main conclusions regarding the role of environmental heterogeneity and the relative importance of variation in species richness and species turnover remained unchanged (Extended Data Fig. 9).

Discussion

Our findings have three major implications. First, we discovered that increasing the length of environmental gradients by considering multiple instead of single ecosystem types increases the strength of the relationship between biodiversity and ecosystem functioning. These results go beyond previous observational studies that have investigated diversity–productivity relationships in grassland, savannah and forest ecosystems[20,24,25] by showing that, regardless of trophic level or type of ecosystem function, environmental heterogeneity strengthens the relationship between species richness and ecosystem functioning across broad environmental gradients. Our results therefore suggest that the relationship between species richness and ecosystem functioning may be generally stronger at the landscape scale than at smaller scales. The importance of landscape-scale diversity for ecosystem functioning may be particularly pronounced on tropical mountains, given their extraordinary biological and cultural diversity and small-scale mosaic of different ecosystem types[35]. In turn, our results indicate that environmental homogenization weakens the relationship between species richness and ecosystem functioning. In the case of our study region, this is particularly alarming, as there is an ongoing and accelerating homogenization of landscapes due to land grabbing and land-use intensification in sub-Saharan Africa[36,37]. Maintaining the integrity and functionality of ecosystems in the Kilimanjaro region therefore calls for policies that support localized agricultural practices (such as traditional agroforestry systems[38–41]) by integrating traditional knowledge[42], strengthening local institutions and empowering local stakeholders[43]. Such management strategies can help counteract landscape homogenization by promoting a fine-grained mosaic of diverse ecosystem types, thus sustaining high levels of landscape heterogeneity. This could benefit both biodiversity and people by promoting the long-standing diversity of ecosystems on tropical mountains, its associated biocultural diversity[35] and a multitude of key contributions of nature to people[44–47].

Second, our analysis shows that, despite high species turnover, the contribution of diversity to variation in ecosystem functioning along the elevational gradient was more strongly related to variation in species richness than to species turnover. This result is unexpected because previous studies have suggested that species turnover is the main factor determining the effect of diversity on ecosystem functioning in heterogeneous environments[5,26–28,48]. Our findings suggest that assembly mechanisms that shape local species richness can be more important for the relationship between biodiversity and ecosystem functioning in heterogeneous environments than other assembly mechanisms, such as species sorting[17,18]. Accordingly, variation in ecosystem functioning across the elevational gradient of Mt Kilimanjaro may be primarily related to environmental factors that control local species coexistence via niche availability and partitioning[16,18,19]. A previous study has shown that the cross-taxon species richness along the elevational gradient of Mt Kilimanjaro is primarily controlled by mean annual temperature[31]. This suggests that temperature-driven mechanisms that enhance local species coexistence (for instance, via improved resource-use efficiency and reduced metabolic costs in warm environments[49,50]) may be one driver of ecosystem functioning along broad environmental gradients. Similar mechanisms may also shape other highly diverse ecosystems on tropical mountains that are characterized by steep temperature gradients[51].

Third, our results indicate that the high variability reported for the relationship between biodiversity and ecosystem functioning in previous observational studies[13] might be partly related to variability in the degree of environmental heterogeneity. In the context of our study system, the large contribution of diversity to variation in ecosystem functioning is most likely related to the broad range of environmental conditions and to the high diversity of ecosystem types on Mt Kilimanjaro. The strong increase in the contribution of diversity to variation in ecosystem functioning with environmental heterogeneity demonstrates that this factor needs to be considered to upscale the relationship between biodiversity and ecosystem functioning from small-scale experiments to real landscapes. Nevertheless, a key limitation of our correlative analysis is that we cannot disentangle the causal direction of the studied relationships between biodiversity and ecosystem functioning. Thus, even though our findings based on a broad range of taxa and ecosystem functions in naturally assembled communities are in line with experiments[1], we are limited in identifying the underlying mechanisms. However, previous work in non-experimental systems indicates that, regardless of spatial scale, both causal directions are equally likely[24] and that strong feedbacks exist between species richness, ecosystem functioning and environmental conditions (for example, climate or resource availability)[20]. Assessing how these feedbacks shape the relationship between biodiversity and ecosystem functioning from local to global scales remains a frontier for future research.

Conclusion

Our analyses reveal that environmental heterogeneity strengthens the effect of diversity on ecosystem functioning and that species richness seems to be more strongly related to ecosystem functioning than species turnover in this non-experimental system. These results imply that environmental homogenization can fundamentally weaken the relationship between biodiversity and ecosystem functioning and that maintaining the functionality of ecosystems requires the promotion of species-rich ecological communities.

Methods

Study area. We conducted the study on the southern and southeastern slopes of Mt Kilimanjaro (Tanzania, East Africa; 2° 45′–3° 25′ S, 37° 00′–37° 43′ E)[32]. Mt Kilimanjaro rises from the lowland at an elevation of 700 m a.s.l. to a snow-capped summit at an elevation of 5,895 m a.s.l. The mean annual temperature decreases with a lapse rate of ~0.87 °C per 100 m at elevations below 2,200 m a.s.l. and with a lapse rate of ~0.42 °C per 100 m at higher elevations (Extended Data Fig. 1)[32,52,53]. The mean annual precipitation shows an unimodal relationship with elevation and peaks in the forest belt at an elevation of ~2,200 m a.s.l. (Extended Data Fig. 1)[32,52,53]. Moreover, precipitation is characterized by a main rainy season occurring from March through May and more variable short rains around November[32,52,53]. Owing to the long history of human settlement in the Kilimanjaro region, natural ecosystems in the lowlands have been subject to various forms of land use and associated disturbance regimes including fire, logging and agroforestry practices[52,53]. Ecosystems above 2,700 m a.s.l. have been protected as a national park since 1973 (Mt Kilimanjaro National Park), while the ecosystems above 1,800 m a.s.l. were included in the national park in 2006 (ref. [32]).

Study design. We collected data on a total of 71 study sites along five elevational transects (pairwise distance, 20.7 ± 11.7 km (mean ± s.d.); range, 0.13–54 km)[32]. The study sites comprise six near-natural and seven anthropogenic ecosystem types: savannah ($n = 6$) and maize fields ($n = 6$) at elevations from 850 to 1,150 m a.s.l.; lower montane forest ($n = 6$), traditional homegarden agroforestry systems ($n = 5$), coffee plantations ($n = 6$) and grassland ($n = 7$) at elevations from 1,150 to 2,100 m a.s.l.; natural ($n = 5$) and disturbed *Ocotea* forest ($n = 5$) at elevations from 2,150 to 2,750 m a.s.l.; natural ($n = 5$) and disturbed *Podocarpus* forest ($n = 5$) at elevations from 2,750 to 3,000 m a.s.l.; natural ($n = 4$) and disturbed *Erica* forest ($n = 6$) at elevations from 3,400 to 4,000 m a.s.l.; and alpine *Helichrysum* vegetation ($n = 5$) at elevations from 3,850 to 4,550 m a.s.l. Detailed descriptions of the vegetation and land-use types on Mt Kilimanjaro are given in previous work[32,52,53].

Environmental variables. The methods to quantify the environmental variables used in the present study have been described in detail in previous work[32,53,54]. Here we provide a brief summary with reference to the relevant studies.

Climate variables. We used mean annual temperature, mean annual precipitation and relative humidity to quantify climatic conditions at the study sites[53,54]. To do so, we installed combined temperature and humidity sensors ~2 m above the ground

Table 1 | Environmental heterogeneity increases the effect of diversity on ecosystem functioning via variation in species richness and species turnover

Pathway	Effect size (95% CrI)	2lnBF	Proposed interpretation
Environmental heterogeneity			
Total effect: $\theta_{H\to Y}+\theta_{H\to R\to Y}+\theta_{H\to T\to Y}$	1.3 (0.96, 1.7)	14	Environmental heterogeneity causes an overall increase in the diversity effect on ecosystem functioning
Direct effect: $\theta_{H\to Y}$	0 (−0.41, 0.016)	−3.3	The effect of environmental heterogeneity on the diversity effect is entirely mediated by variation in species richness and species turnover
Effect via variation in species richness: $\theta_{H\to R\to Y}$	1.0 (0.63, 1.5)	16	Variation in species richness primarily mediates diversity effects on ecosystem functioning in heterogeneous environments
Effect via species turnover: $\theta_{H\to T\to Y}$	0.32 (0, 0.64)	5.7	Species turnover is less important than variation in species richness for diversity effects on ecosystem functioning in heterogeneous environments
Contrast of indirect effects: $\theta_{H\to R\to Y}$ versus $\theta_{H\to T\to Y}$	0.72 (0.093, 1.5)	8.5	Environmental factors promoting local species coexistence are more important for variation in ecosystem functioning than species sorting
β-diversity components			
Variation in species richness: $\theta_{R\to Y}$	1.7 (1.4, 2.1)	15	Variation in species richness strongly contributes to variation in ecosystem functioning
Species turnover: $\theta_{T\to Y}$	1.1 (0.79, 1.5)	14	Species turnover strongly contributes to variation in ecosystem functioning
Contrast of direct effects: $\theta_{R\to Y}$ versus $\theta_{T\to Y}$	0.55 (0.13, 1.0)	11	Variation in species richness is more important for variation in ecosystem functioning than species turnover

The table shows effect sizes (θ) estimated by the Bayesian hierarchical structural equation model (medians and 95% CrIs based on the posterior distribution of the estimated model parameters), 2lnBF as a measure of evidence for a given effect, and the proposed interpretation of the effects. The effect sizes reflect the expected change in the response variable for a 1% change in the predictor variable (for example, $\theta_{R\to Y}=1.7$ means that an increase of 10% in variation in species richness causes an increase of 17% in the diversity effect). Values of 2lnBF less than 2 indicate no support, values between 2 and 6 indicate positive support, values between 6 and 10 indicate strong support, and values above 10 indicate decisive support.

at all study sites[32]. The sensors measured temperature and humidity in 5 min intervals for ~2 years. We calculated mean annual temperature (°C) and relative humidity (%) as the average of all measurements per study site[32]. We interpolated mean annual precipitation (mm yr^{-1}) across the study area using a co-kriging approach based on a 15-year dataset from a network of about 70 rain gauges on Mt Kilimanjaro[31,32,54].

Land-use variables. We used biomass removal, agricultural inputs and landscape composition to quantify the land-use intensity at and around the study sites[32]. For each study site, we calculated the annual removal of plant biomass by taking the average of standardized estimates of ploughing, mowing, cattle grazing, fire events, logging and firewood collection[32]. We estimated ploughing on an ordinal scale (no ploughing, ploughing by hand and ploughing with a tractor)[32]. All other variables were expressed as the percentage of the standing biomass removed per year. We estimated agricultural inputs for each study site by taking the average of standardized estimates of irrigation, fertilization, insecticide, fungicide and herbicide treatments[32]. For these variables, we used an ordinal scale (no to very low, medium or high input)[32]. We measured landscape composition as the proportion of the landscape with agriculturally managed habitats within a 1.5 km radius of the study sites[32]. The classification into natural and managed habitats was based on a land-cover classification of the Kilimanjaro region that identified 27 different habitat types in the study area (18 natural and 9 managed habitat types)[32].

Soil variables. We used organic carbon, pH, C/N ratio, N/P ratio and available water capacity to characterize soil properties[32]. To quantify organic carbon, we sampled surface litter and soil at depths of 0 to 5 cm at five locations per study site[32]. We air-dried material from both layers before further processing. We sieved the soil (2 mm mesh) before grinding it with a mixer mill (MM200, Retsch)[32]. To determine elemental C (that is, organic carbon), we analysed all samples using continuous-flow isotope ratio mass spectrometry with a dry combustion elemental analyser (Costech International) fitted with a zero-blank autosampler coupled to a ThermoFinnigan DeltaPlus-XL[32]. We averaged the individual values for soil and litter for each study site[32].

To quantify soil pH, C/N ratios and N/P ratios, we took soil samples from soil pits on a horizon basis and in 10 cm intervals using a standard soil auger[32]. We sieved the soil samples (2 mm mesh) to remove roots and plant materials. We then dried the samples at 105 °C for 24 h and ground them for further analysis[32]. We analysed the total C and N contents of the soil samples using an automated dry combustion C:N analyser (Vario EL, Elementar) at 950 °C (ref. [32]). We analysed the total P content using inductively coupled plasma optical emission spectrometry (Spectro Analytical Instruments) after preparative pressure digestion (HNO_3 digestion)[32]. We measured soil pH in a KCl solution (1 M, 1:2.5) using a pH electrode[32]. For each study site, we averaged the estimates for the horizons and 10 cm intervals across soil depths of 0 to 50 cm.

To quantify available water capacity, we took soil samples using soil sampling rings (100 cm^3) from different horizons along the soil profile at 12 of the study sites and from the topsoil of 5 additional study sites[32]. We used these soil samples to measure the water retention at different matric potential levels (pF)[32]. We then estimated water retention curves using the van Genuchten equation[55] and calculated the available water capacity (in mm) per horizon as the water content at pF 4.2 minus the water content at pF 1.8 (ref. [32]). We calculated the total available water capacity by summing the available water capacity of the individual horizons down to 100 cm, or until bedrock was reached[32]. In addition, we took bulk soil samples either from individual horizons of the soil profiles or from soil auger samples at different depth intervals down to at least 50 cm (or until bedrock was reached) at all study sites[32]. For these soil samples, we measured soil organic carbon, cation exchange capacity and base saturation. We then used these variables together with the habitat type as predictor variables in a random forest model to predict the available water capacity for all other soil samples ($r^2=0.88$; root mean square error, 4.93)[32]. We then calculated the total available water capacity in the same way as for the measured samples[32].

Data on ecosystem functions. Our approach requires information about the actual contribution of each species to ecosystem functioning in each community. For 17 of the 22 functions, we had direct estimates of species-specific functional contributions in each community. For the 5 functions for which direct estimates of species-specific functional contributions were not available (that is, for fine root biomass of woody plants, fine root production, biomass of microorganisms, litter decomposition and dung decomposition), we used site-level data on ecosystem functioning (that is, aggregate values of ecosystem functions for each community) 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. We thus assumed for these functions that the functional contribution of a species was proportional to its relative abundance or biomass in a given community[33,34].

Biomass stocks. For springtails, ants, bees, parasitoid wasps, non-bee and non-ant aculeate wasps, moths, dung beetles, birds, insectivorous bats, fruit bats and large

terrestrial mammals, we calculated species biomass stocks at each study site by combining data on species abundances at each study site with data on species per capita mass. Data on species abundances at the study sites were recorded using standardized approaches with taxon-specific sampling methods, which have been described in previous studies[31,32,56]. We derived species-specific estimates of per capita mass for birds, insectivorous bats, fruit bats and large terrestrial mammals from the literature[57–59]. For dung beetles, we directly measured species-specific per capita mass of all species using a precision scale. We derived species-specific estimates of per capita mass for ants, bees, aculeate wasps, parasitoid wasps, moths and springtails by applying allometric equations to morphometric measures. For ants we used head length[60], for bees the intertegular distance[61–63], and for the two wasp groups, moths and springtails the total body length of specimens (excluding the ovipositor/sting of wasps)[64] as morphometric target measures. Morphometric measurements were taken from up to ten randomly selected individuals per species using a binocular microscope with a calibrated ocular micrometre[62]. The individual biomass calculated by using allometric equations closely fits the true biomass determined with a precision scale[60–64].

For woody plants, we estimated species-specific aboveground biomass stocks at each study site by applying pantropical allometric equations to measures of plant height, diameter at breast height and wood density, which were taken for all woody plant individuals at the study sites (that is, trees and shrubs)[65]. We included all shrub (diameter at breast height < 10 cm) and tree (diameter at breast height ≥ 10 cm) individuals that were taller than 1.3 m and calculated species-specific aboveground biomass stocks by summing individual biomass estimates for each species at each study site[65]. Because aboveground and belowground biomass of woody plants follow a close isometric relationship at the individual and community levels[66], we estimated species-specific fine root biomass stocks of woody plants (<2 mm in diameter) by allocating the total fine root biomass at each study site proportional to the relative aboveground biomass of each species at each study site. We estimated the total fine root biomass of woody plants at each study site by analysing 10 to 15 randomly distributed soil cores (3.5 cm in diameter and 40 cm in depth) and differentiating living from dead fine roots[32].

We quantified the total microbial biomass at each study site from the upper 10 cm of the soil[67]. Likewise, soil microorganisms (including Bacteria and Archaea) were sampled at each study site from the upper 10 cm of the soil (a detailed description is given in a previous publication)[32]. We assumed that read frequencies reflect the relative abundances of each molecular operational taxonomic unit (hereafter referred to as species)[32]. We estimated the species-specific contribution to the total microbial biomass (mg cm^{-3}) by allocating the total microbial biomass proportional to the relative abundances of the species at each study site.

The total biomass stocks were given by the sum of the species-specific biomass estimates of each study site.

Process rates. Process-specific protocols were used to measure seed dispersal by birds, pollination by birds, pollination by insects, brood parasitism by insects, resource use by ants, litter decomposition by microorganisms, dung decomposition by dung beetles and fine root production of woody plants.

We recorded data on seed dispersal and pollination by birds as well as pollination and brood parasitism by insects using standardized approaches that have been described in previous studies[32,68]. In brief, we studied seed dispersal and pollination by birds by monitoring bird–fruit and bird–flower interactions on a plot of 30 m × 100 m at each site. We sampled each site once over four consecutive days for a total of 25 h (ref. [68]). We observed birds using binoculars to record interactions with fruiting and flowering plants. We recorded the number of visits of each bird species to each fruiting or flowering plant species and recorded their behaviour[68]. On the basis of the bird–fruit and bird–flower interaction data, we calculated species-specific contributions to seed dispersal and pollination as the number of visits to all fruiting and flowering plants by each bird species, considering only visits that were classified as legitimate seed removal or pollination events—that is, swallowing or carrying away of fruits from mother plants, as well as pollen uptake.

We studied pollination by insects by repeatedly monitoring insect–flower interactions on a plot of 100 m × 100 m at 19 study sites[68,69]. During each sampling round at a given study site, we conducted a four-hour transect walk during which we moved slowly through the vegetation and recorded each interaction in which an insect touched the reproductive part of a plant species (herbaceous plants and bushes up to 9 m tall)[68,69]. We thus assumed that all flower-visiting insects contribute to pollination. We restricted our sampling to major groups of pollinators (including Apiformes, the paraphyletic group of non-bee aculeates, Symphyta and Syrphidae)[68,69]. We excluded other Diptera from the analyses, for which identification below the family level was not feasible. On the basis of the insect–flower interaction data, we calculated species-specific contributions to pollination as the number of visits to all flowering plants by each insect species, considering only visits of insects that touched plant reproductive organs. Because the sites were monitored multiple times, we calculated all derived variables on the basis of the individual transect walks and then averaged the values across the transect walks for each site.

We studied parasitism of host insects (bees and wasps) by parasitic insects by repeatedly monitoring standardized trap nests at 24 study sites over a period of 14 months[70]. At each study site, we installed eight trap nests arranged in four pairs that were placed 140 cm above the ground. At study sites with trees, we installed two pairs of traps in the lower canopy (up to ~25 m high) and two pairs above the ground[70]. We built trap nests with a mixture of ~120 internodes of common reed (*Phragmites australis*) and Japanese knotweed (*Fallopia japonica*) with diameters of 2–25 mm and lengths of 20 cm (ref. [70]). We used glue to prevent ants from plundering the nests. We controlled the trap nests monthly and replaced occupied nests with new internodes. We closed occupied internodes with metal nets and placed them in a hatching box on the study site. To record parasitism rates, we cut open the internodes in the laboratory after hatching[70]. On the basis of the parasite–host interaction data, we calculated species-specific contributions to parasitism as the number of brood cells that were attacked by each parasite species. Because the sites were monitored multiple times, we calculated all derived variables on the basis of the monthly samples and then averaged the values across the samples for each site.

We studied resource use by ants by using bait experiments[71]. At each study site, we placed thirty 50 ml Falcon tubes that were filled with 10 ml of a nutrient solution (sugar, sugar–protein, protein, water, salt and oil; five replicates per nutrient) along three 50 m transects at ground level. After two hours, we collected the baits and recorded the number of individuals of each ant species at each bait[71]. On the basis of the ant occurrence at the baits, we calculated species-specific contributions to resource use as the proportion of baits detected by each ant species. When more than one ant species was recorded at a bait, we allocated the species-specific contributions to resource use in proportion to the relative abundance of the respective ant species at that bait.

We studied litter decomposition rates by using standardized litter bags with dried maize straw (10 cm × 15 cm, 20 µm × 20 µm mesh size, 5 ± 0.05 g maize husks, three bags per study site), which were placed at each study site and collected after 69 to 86 days[32]. We dried and processed the leaves following protocols described in previous work[32]. For logistic reasons, bags at lower elevations were partly exposed longer than bags at higher elevations[32]. To account for these differences, we calculated decomposition rates per day. Decomposition rates (k) were calculated as $k = -\ln(m_{LOI}/m_{OAF})/t$, 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[32]. We averaged the decomposition rates per study site. As we did not have direct measures of species-specific contributions to litter decomposition, we estimated the specific contribution of each microbial species to decomposition at each site on the basis of the relative abundance (approximated from read frequencies) of each species at each site (see the paragraph on microbial biomass under 'Biomass stocks' for additional details).

We studied dung decomposition rates by placing 750 g of fresh cow dung (ca. 120 g dry weight) at each study site in two different seasons[32,56]. After 15 days, the remaining dung was collected, dried at 72 °C for one week and weighed. Analogous to litter decomposition rates, dung decomposition rates were calculated for each study site as $k = -\ln(m_{remaining}/m_{original})/t$, where $m_{remaining}$ is the remaining dry weight, $m_{original}$ is the original dry weight and t is the number of days the dung has been exposed. We averaged the decomposition rates per study site. As we did not have direct measures of species-specific contributions to dung decomposition, we estimated the specific contribution of each dung beetle species to decomposition at each site on the basis of the relative biomass of each species at each site.

We studied the fine root production of woody plants with the ingrowth core approach. Ten soil ingrowth cores per study site were installed to 40 cm depth. After extraction of the soil with a soil core sampling device 3.5 cm in diameter, we manually removed all visible roots and refilled the holes with the original root-free soil with care to keep soil conditions as natural as possible, and we resampled after one year. Fine roots were extracted in the laboratory, sorted into live and dead biomass and dried at 70 °C for 48 hours. We calculated fine root production as ingrown fine root mass (living and dead) divided by the length of time between the start of recolonization and harvest. We extrapolated these values to one year to obtain an estimate of annual fine root production (Mg ha^{-1} yr^{-1}). As we did not have direct measures of species-specific contributions to fine root production, we estimated species-specific fine root production of woody plants by allocating the total fine root production at each study site proportional to the relative aboveground biomass of each species at each study site.

Quantifying the effect of diversity on ecosystem functioning. The framework to quantify the contribution of diversity to variation in ecosystem functioning builds on a community matrix $\mathbf{F}$ ($n \times s$), which describes the contribution of s species to a given ecosystem function at n study sites (hereafter referred to as communities). Each element f_{ij} of matrix $\mathbf{F}$ describes the contribution of species j to a given ecosystem function at study site i. Furthermore, let $\mathbf{P}$ ($n \times s$) be a binary matrix with the same dimensions as $\mathbf{F}$ in which element $p_{ij} = 1$ if $f_{ij} > 0$ and $p_{ij} = 0$ otherwise. Matrix $\mathbf{P}$ represents a species incidence matrix. We denote the complement of the species incidence matrix $\mathbf{P}$ as $\mathbf{Q} = 1 - \mathbf{P}$. Therefore, $q_{ij} = 1$ if $f_{ij} = 0$ and $q_{ij} = 0$ otherwise. Furthermore, we denote the sum of $\mathbf{P}$ and $\mathbf{Q}$ as $\mathbf{O} = \mathbf{P} + \mathbf{Q}$. Thus, in matrix $\mathbf{O}$ all elements $o_{ij} = 1$. The total difference in the magnitude of a given ecosystem function between a pair of communities i and j is then given by 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 a given ecosystem function between two communities i and j that arises from changes in the functional contributions of species that are shared between both communities is given by element Δs_{ij} of the $n \times n$ square matrix $\Delta\mathbf{S} = \mathbf{FP}^{\mathrm{T}} - \mathbf{PF}^{\mathrm{T}}$. Finally, the difference in the magnitude of a given ecosystem function between two communities i and j that arises from the combined effects of variation in species richness and species turnover between communities is given by element Δd_{ij} of the $n \times n$ square matrix $\Delta\mathbf{D} = \mathbf{FQ}^{\mathrm{T}} - \mathbf{QF}^{\mathrm{T}}$. It follows that:

$$\Delta f_{ij} = \Delta d_{ij} + \Delta s_{ij} \tag{1}$$

All three components in equation (1) have the dimension of the respective ecosystem function and an expected value of zero under the null hypothesis of no overall difference in function between communities i and j ($\Delta f_{ij} = 0$), no difference in function due to variation in species richness and species turnover ($\Delta d_{ij} = 0$) or no difference in function due to variation in the functional contributions of shared species ($\Delta s_{ij} = 0$). Consequently, all three components can equally be positive or negative, and there is a potential for diversity and shared species components to cancel each other, resulting in a net difference in function of zero. Note that equation (1) is equivalent to the 'community-assembly-decomposition' of the Price equation in Bannar-Martin et al.[14]. However, this formulation overcomes the limitations of previous approaches[14,30], as it allows for comparisons between communities, regardless of whether these communities have species in common. This is a prerequisite to study the contribution of diversity to variation in ecosystem functioning across broad environmental gradients with complete species turnover.

On the basis of equation (1), we can quantify the relative contribution of diversity to variation in ecosystem functioning between communities (that is, the diversity effect) as[72]:

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

where $|\Delta d_{ij}|$ and $|\Delta s_{ij}|$ are the absolute values of Δd_{ij} and Δs_{ij}, respectively. We use absolute values, because we are interested in the absolute differences between communities and not whether community i has a higher value than j or vice versa. In addition, Δd_{ij} and Δs_{ij} can take negative and positive values, and simply taking the mean of these values would obscure the overall contribution of both components. The diversity effect is a unitless metric that ranges between 0 and 1. The diversity effect equals 0 if all variation in ecosystem functioning between communities arises from variation in the functional contributions of those species that are shared between communities (that is, due to differences in abundance or individual performance of shared species; Fig. 1c). Conversely, the diversity effect equals 1 if all variation in ecosystem functioning arises from the combined effects of variation in species richness and species turnover between communities (Fig. 1a,b). The shared species effect Z is the exact complement of the diversity effect (that is, $Z = 1 - Y$).

Note that variation in the functional contributions of shared species between communities in terms of biomass can be due to variation in abundance or individual performance. We expected that in organisms with low phenotypic plasticity in individual body mass (for example, animals), variation in the functional contributions of shared species between communities would be mainly driven by variation in abundance, whereas in organisms with high phenotypic plasticity (for example, plants), variation in the functional contributions of shared species between communities can be due to variation in abundance or individual performance or both. In our case, the only two functions for which data on biomass were resolved at the individual level were dung beetle biomass (and implicitly decomposition by dung beetles) and woody plant aboveground biomass (and implicitly fine root biomass and fine root production). Our measure of the shared species effect thus relates to changes in species abundance in the majority of the studied ecosystem functions.

Quantifying variation in species richness and turnover. To disentangle whether the contribution of diversity to variation in ecosystem functioning between n communities is driven by variation in species richness, species turnover or both, we continue with the above notation and partition the variation in species composition (β) into variation due to differences in species richness (R) and due to species turnover (T) between the n communities[22,23]. The species richness and turnover components form a true partition of the total variation in species composition[23] so that $\beta = R + T$. To estimate the total variation in species composition and its two components, we use the Jaccard index, which can be calculated on the basis of the species incidence matrix $\mathbf{P}$ and its complement $\mathbf{Q}$. For a given pair of communities i and j, the number of species that are shared between both communities is given by element a_{ij} of the $n \times n$ matrix $\mathbf{A} = \mathbf{PP}^{\mathrm{T}}$, the number of species that are unique to community i is given by element b_{ij} of the $n \times n$ matrix $\mathbf{B} = \mathbf{PQ}^{\mathrm{T}}$ and the number of species that are unique to community j is given by element c_{ij} of the $n \times n$ matrix $\mathbf{C} = \mathbf{QP}^{\mathrm{T}}$. On the basis of this set of equations, the total variation in species composition (β), the richness component (R) and the turnover component (T) can be written as:

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

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

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

Quantifying environmental heterogeneity. We quantified environmental heterogeneity on the basis of a combination of 11 variables related to climatic conditions (mean annual temperature, mean annual precipitation and relative humidity), land use (biomass removal, agricultural inputs and landscape composition) and soil properties (organic carbon, pH, C/N ratio, N/P ratio and available water capacity). To do so, we first calculated the environmental distance between sites using the Gower distance based on the combination of all environmental variables. The Gower distance between two sites i and j equals the mean difference in environmental conditions across variables after standardization of the variables by their ranges,

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

where n is the number of included environmental variables, and x_{ik} and x_{jk} are the values of environmental variable k on study sites i and j. The Gower distance has desirable properties to quantify environmental distance on the basis of multiple environmental variables, because it is less sensitive to extreme values than the Euclidean distance. Moreover, the standardization of the environmental variables by their ranges results in an equal contribution of the variables to the distance and yields an empirical maximum value of the distance function that equals one. This facilitates the interpretation of the metric. Because the data for some environmental variables were missing for some study sites, we calculated the pairwise distances by applying a pairwise deletion of missing observations. We defined environmental heterogeneity (H) as the mean environmental distance across the n study sites,

$$H = \frac{2}{n\,(n-1)} \sum_{i<j}^{n} d_{ij}.$$

The multivariate index of environmental heterogeneity was largely insensitive to the exclusion of single environmental variables (Extended Data Fig. 6).

Statistical analysis. We quantified the diversity effect separately for each of the 22 ecosystem functions. To assess the role of environmental heterogeneity, we quantified the diversity effect on the basis of comparisons between communities within the same ecosystem type (that is, within each of the ecosystem types) and between all communities across the ecosystem types covered by the elevational gradient (that is, across ecosystem types; Extended Data Fig. 4). Likewise, we calculated the richness and turnover components of β-diversity (that is, R and T) separately for each of the 22 ecosystem functions on the basis of comparisons between communities within and across ecosystem types (Extended Data Fig. 4). To obtain a measure of uncertainty for the estimate of the diversity effect, we used a bootstrap procedure, in which we resampled a subset of 80% of the communities without replacement ($n = 1{,}000$ replicates) following Manly[73]. We did not sample with replacement, because duplication of samples is not useful in a dissimilarity context (the dissimilarity of a sample with itself is zero). We applied the resampling procedure to each of the 22 ecosystem functions and calculated the medians, as well as the 50% and 95% CIs. Finally, we calculated environmental heterogeneity (H) separately for each of the 22 ecosystem functions on the basis of comparisons between communities within and across ecosystem types (Extended Data Fig. 6).

We analysed the effect of diversity on variation in each of the ecosystem functions using a Bayesian hierarchical structural equation model (Supplementary Note 1). In this structural equation model, we treated environmental heterogeneity (H) as an exogenous variable. We treated the species richness and turnover components of β-diversity (R and T, respectively) as well as the diversity effect (Y) as endogenous variables (Fig. 3a). The model included all potential direct effects of H on R and T, as well as on Y. Moreover, the model included the effects of R and T on Y. We also included a covariance term between R and T to account for correlated errors due to common unmeasured sources of variance. To account for the non-independence between the pairs of diversity effect sizes for each ecosystem function (within and across ecosystem types), we included the identity of each function as a random factor in the model ($n_{\text{functions}} = 22$). In particular, the model that we developed contained three submodels, one for each of the three

endogenous response variables. In its most general form, the model can be written as:

$$\mu_{il} = \alpha_l + \sum_j \theta_{jl} X_{ijl} + f_{k[i]l} \quad (6)$$

$$\alpha_l \sim \text{Normal}\left(0, 10^4\right) \quad (7)$$

$$f_{kl} \sim \text{Normal}\left(0, \sigma^2_{fl}\right) \quad (8)$$

$$\sigma^2_{fl} \sim \text{Scaled inverse gamma}\,(s, \text{d.f.}) \quad (9)$$

where μ_{il} is the expected value of the ith observation of response variable l, α_l is the intercept, $\mathbf{X}_l$ is a matrix with fixed effects and an associated vector of parameters $\boldsymbol{\theta}_l$, and f_{kl} is a random effect for the kth ecosystem function, which is normally distributed around 0 with variance σ^2_{fl}. We used an uninformative normal prior with a variance of 10^4 for the intercept α. For the variance of the random effect, we used a weakly informative scaled inverse gamma prior[74] with scale $s = 1$ and two degrees of freedom (d.f. = 2), which for the standard deviation follows a half-t distribution, $\sigma_f \sim st^+_{\text{d.f.}}$. To account for the fact that variation in species richness (R) and species turnover (T) are potentially correlated, we modelled these response variables with a multivariate normal distribution around μ_{il} and residual covariance $\boldsymbol{\Sigma}_\varepsilon$:

$$y_{il} \sim \text{Normal}\,(\mu_{il}, \Sigma_\varepsilon) \quad (10)$$

$$\boldsymbol{\Sigma}_\varepsilon \sim \text{Scaled inverse Wishart}\,(s, \text{d.f.}) \quad (11)$$

where $\boldsymbol{\Sigma}_\varepsilon$ is a 2×2 variance–covariance matrix. We used a non-informative scaled inverse Wishart prior[75] with scale $s_i = 1$ and d.f. = 2. This prior follows a half-t distribution for the residual standard deviation, $\sigma_{ii} \sim st^+_{\text{d.f.}}$, and has a marginal uniform prior distribution for the correlation parameter ρ_{ij}. We modelled the diversity effect (Y) with a normal distribution around μ_i and residual variance σ^2_ε. Again, we used a weakly informative scaled inverse gamma prior with scale $s = 1$ and d.f. = 2 for the residual variance of Y:

$$y_i \sim \text{Normal}\left(\mu_i, \sigma^2_\varepsilon\right) \quad (12)$$

$$\sigma^2_\varepsilon \sim \text{Scaled inverse gamma}\,(s, \text{d.f.}) \quad (13)$$

To separate informative from non-informative paths, we used a Bayesian indicator variable selection with global adaptation[68,76,77]. Indicator variable selection combines the effect size β_j with an indicator variable I_j to denote whether the regression parameters θ_j are in the model or not (where $I_j = 1$ indicates presence and $I_j = 0$ indicates absence of covariate j in the model). We then set $\theta_j = I\beta_j$ assuming that the indicators and effects are independent a priori, so $P(I_j, \beta_j) = P(I_j)P(\beta_j)$, and place independent priors on each I_j and β_j[68,76,77]:

$$P\left(I_j = 1\right) \sim \text{Bernoulli}\,(0.5) \quad (14)$$

$$\beta_j \,|\, \left(I_j = 1\right) \sim \text{Normal}\left(0, \sigma^2_\beta\right) \quad (15)$$

$$\sigma^2_\beta \sim \text{Scaled inverse gamma}\,(s, \text{d.f.}) \quad (16)$$

We set the prior inclusion probability $P(I_j = 1)$ to 0.5. The effect sizes β_j were sampled from a normal distribution with $\mu_\beta = 0$ and variance σ^2_β. As for the other variance parameters, we used a weakly informative scaled inverse gamma prior with scale $s = 1$ and d.f. = 2 for σ^2_β. This form of global adaptation has the advantage of facilitating the tuning of the variable selection, because the distribution of each θ_j is shrunk towards the correct region of the parameter space by the other parameters in the vector of regression coefficients $\boldsymbol{\theta}$ in the model[76].

To facilitate model convergence and the variable selection, we scaled all variables to zero mean and unit variance. However, we back-transformed the coefficients for the presentation of the results[78], because all variables have theoretical ranges between 0 and 1. The estimated path coefficients θ_j therefore reflect the expected change in the response variable for a 1% change in the predictor variable (for example, $\theta_{R \to Y} = 1.7$ means that an increase of 10% in variation in species richness causes an increase of 17% in the diversity effect).

We used the posterior distribution of the model parameters to predict the effect of diversity on ecosystem functioning for the mean observed environmental heterogeneity for comparisons within and across ecosystem types (mean: $H_{\text{within}} = 0.14$ versus $H_{\text{across}} = 0.31$). To test whether the effects of environmental heterogeneity on the contribution of diversity to variation in ecosystem functioning are mediated by variation in species richness or species turnover, we quantified the direct effect of environmental heterogeneity on the diversity effect, as well as the indirect effects that were mediated by variation in species richness and species turnover. We calculated indirect effects as the product of path coefficients leading to the diversity effect. For instance, the indirect effect of environmental heterogeneity on the diversity effect via variation in species richness is calculated as $\theta_{H \to R \to Y} = \theta_{H \to R} \times \theta_{R \to Y}$. To assess whether variation in species richness or species turnover had a stronger effect on the contribution of diversity to variation in ecosystem functioning, we also directly compared their effects using contrasts (that is, $\theta_{H \to R \to Y}$ versus $\theta_{H \to T \to Y}$ and $\theta_{R \to Y}$ versus $\theta_{T \to Y}$).

We used Bayes factors (BFs) as a measure of evidence for a given effect[76,79]. We calculated BFs as the degree of shift in prior beliefs about a given effect, which can be calculated by dividing posterior odds by prior odds:

$$\text{BF} = \frac{\text{Posterior odds}}{\text{Prior odds}} = \frac{P_{\text{posterior}} / \left(1 - P_{\text{posterior}}\right)}{P_{\text{prior}} / \left(1 - P_{\text{prior}}\right)}.$$

For single paths, we calculated the prior odds on the basis of the prior selection probability of each path (that is, $P_{\text{prior}} = 0.5$). For indirect effects involving two paths, we calculated the prior odds on the basis of the product of the prior selection probabilities of the respective paths (that is, $P_{\text{prior}} = 0.5 \times 0.5 = 0.25$). Following Kass and Raftery[79], we $2\ln(x)$-transformed the BF values. Values of 2lnBF less than 2 indicate no support, values between 2 and 6 indicate positive support, values between 6 and 10 indicate strong support, and values greater than 10 indicate decisive support.

We used posterior predictive checks to assess the global fit of the model to the data[80]. As a measure of global model fit, we computed a posterior predictive P value (PPP) that compares the observed standardized root mean squared residuals (SRMR) based on the observed and the model-implied covariance matrices to SRMR generated from the posterior predictive distribution of the model[80]. Values of PPP_{SRMR} close to 0.5 indicate that the model fits the observed covariance matrix, while values close to 0 or 1 indicate the opposite[80]. We report the marginal variance, r_m^2, that is explained by the fixed factors, as well as the conditional variance, r_c^2, that is explained by the fixed and random factors combined as measures of local fit[81,82]. In addition, we provide partial residual plots for visual inspection of model fit (Extended Data Fig. 8). Finally, we provide median estimates along with 50% and 95% CrIs for all estimates as measures of uncertainty.

All analyses were conducted in R (version 4.0.3)[83]. Gower distances for environmental heterogeneity were calculated using the vegan package (version 2.5-7)[84]. The Bayesian model was implemented in JAGS (version 4.3)[85] and run in R through the rjags package (version 4-10)[86]. We ran eight parallel chains for the model. The initial values for the chains were drawn randomly from the prior distributions of the stochastic variables using the LaplacesDemon package (version 16.1.4)[87]. Each chain was run for 135,000 iterations with an adaptive burn-in phase of 10,000 iterations and a thinning interval of 100 iterations, resulting in 1,250 samples per chain, corresponding to 10,000 samples from the posterior distribution. The chains were checked for convergence, temporal autocorrelation and effective sample size using the coda package (version 0.19-4)[88]. The residuals were checked for normality and variance homogeneity. We provide a complete summary of the model output in Extended Data Fig. 7. The structural equation model was visualized using the qgraph package (version 1.6.5)[89].

Sensitivity analyses. We performed several sensitivity analyses to assess the robustness of our results. First, we assessed whether our conclusions are robust to the inclusion or exclusion of functions for which we did not have direct estimates of species-specific contributions to ecosystem functioning. To do so, we re-analysed the data after excluding those functions for which only indirect estimates of species-specific contributions were available (5 of 22 functions). Second, we assessed whether our conclusions are robust to the presence of outliers in the data for each ecosystem function. To do so, we re-analysed the data after excluding study sites with disproportionately high or low levels of ecosystem functions that might affect the estimates of the diversity effect. In particular, we removed for each function those study sites for which values of ecosystem functioning fell outside 1.5 times the interquartile range. Third, we assessed whether our conclusions are robust to the pooling of natural and anthropogenic ecosystem types by analysing the data from natural and anthropogenic ecosystem types separately. Fourth, we assessed to what extent our conclusions are affected by the potentially confounding effects of variation in environmental factors along the elevational gradient (for example, climate or soil conditions). To do so, we statistically modelled the linear or nonlinear elevational trends in the ecosystem functions with generalized additive models with a thin plate spline and second-order penalty $m = 2$ using the R package mgcv (version 1.8-33)[90]. To avoid overfitting, we set the basis dimension to $k = 5$ if $n > 40$ and to $k = 4$ otherwise. For the two functions for which the sites were monitored multiple times (insect pollination and brood parasitism), we included study site as a random factor smooth term in the models. We then detrended the ecosystem functions by calculating the residuals from the fitted elevational trends (Extended Data Fig. 10) and calculated the diversity effect sizes on the basis of the residuals of these models. All of these

sensitivity analyses led to the same conclusions as presented in the main text (Extended Data Fig. 9).

Sampling completeness. We assessed the taxonomic sampling completeness for each of the 22 ecosystem functions at three different sampling grains—that is, at the level of study sites, at the level of ecosystem types (study sites pooled by ecosystem type) and at the level of the entire mountain (all study sites pooled). For each function, we estimated taxonomic sample coverage[91] at each sampling grain on the basis of species abundances as the proportion of the total number of individuals that belong to the species represented in the sample (Extended Data Fig. 2). We estimated sample coverage[83] using the R package iNEXT (version 2.0.20)[92]. For the vast majority of functions, the taxonomic sample coverage was extremely high at all three sampling grains, with a mean sample coverage across functions of 90 ± 15% (mean ± s.d.) at the site level, 94 ± 12% at the ecosystem level and 97 ± 7.5% at the mountain level. We achieved a sample coverage above 80% for 19 of 22 functions at the site level, 19 of 22 functions at the ecosystem level and 20 of 22 functions at the mountain level. The three taxa with the lowest coverage were aculeate wasps (65%, 57% and 72% at the site, ecosystem and mountain levels, respectively), parasitoid wasps (49%, 67% and 78%, respectively) and moths (58%, 73% and 90%, respectively).

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

Data availability

The data that support the findings of this study are available in *Figshare*[93] with the identifier https://doi.org/10.6084/m9.figshare.14544207.

Code availability

The computer code of the analyses is available in *Figshare*[93] with the identifier https://doi.org/10.6084/m9.figshare.14544207. The JAGS code for the Bayesian hierarchical structural equation model is also given in Supplementary Note 1.

Received: 2 February 2021; Accepted: 9 August 2021;
Published online: 20 September 2021

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Acknowledgements

We thank the Tanzanian Commission for Science and Technology, the Tanzania Wildlife Research Institute and the Tanzania National Parks Authority for their support and for granting us access to the Kilimanjaro National Park area. We are grateful to all companies and private farmers that allowed us to work on their land. We thank the KiLi field staff for helping with data collection at Mt Kilimanjaro. This study was conducted within the framework of the Research Unit FOR1246 ('Kilimanjaro ecosystems under global change: linking biodiversity, biotic interactions and biogeochemical ecosystem processes', https://www.kilimanjaro.biozentrum.uni-wuerzburg.de) funded by the Deutsche Forschungsgemeinschaft.

Author contributions

J.A., M.K.P., I.S.-D. and M.S. conceived the study. M.F., A.H. and I.S.-D. initiated the research unit at Mt Kilimanjaro. A.H. established the study sites. C. Bogner, K.B.-G., R.B., M.F., A.H., D.H., B.H., R.K., M.K., Y.K., C.L., T.N., M.K.P., M.S., I.S.-D. and M.T. conceptualized and supervised the data collection. J.N.B., C. Behler, A.C., H.I.D., C.D.E., A.E., S.W.F., F. Gebert, F. Gerschlauer, M.H.-B., A.H., V.K., A. Keller, W.J.K., A. Kühnel, A.V.M., H.K.N., H.P., M.K.P., R.S.P., U.P., J.R., G.R., D.S.C., N.S.-C., A.V., M.G.R.V. and J.Z. collected the data. A.H., C.H., H.I.D., K.M.H., V.K. and J.Z. supported the data collection and fieldwork. J.A. and M.K.P. processed the data. J.A. developed the analytical tools with input from M.S. J.A. analysed the data and wrote the first version of the manuscript with input from M.K.P., I.S.-D., M.S., P.M. and T.M. All authors contributed to subsequent versions of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-021-01550-9.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-021-01550-9.

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Peer review information *Nature Ecology & Evolution* thanks Kathryn Barry, Yahuang Luo and Jean-François Arnoldi for their contribution to the peer review of this work. Peer reviewer reports are available.

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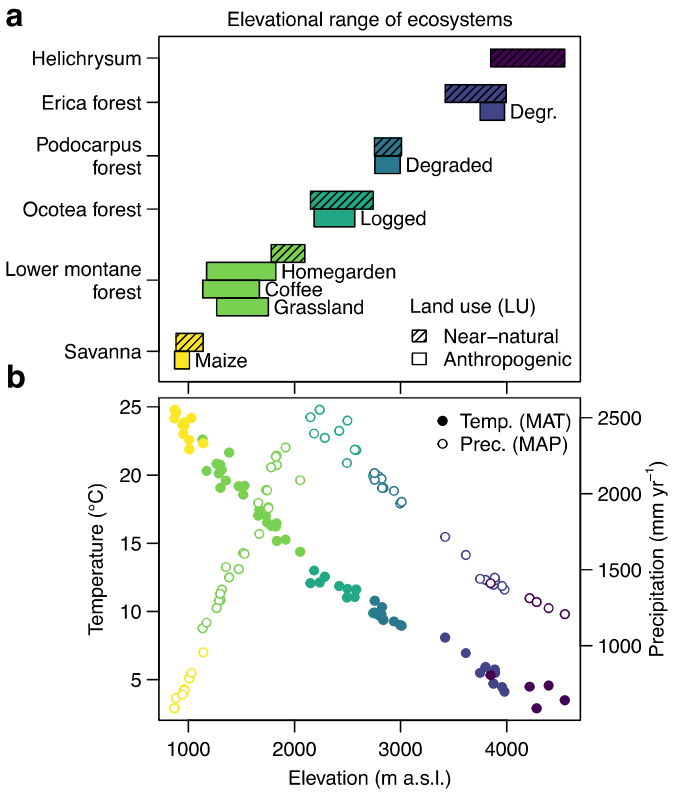
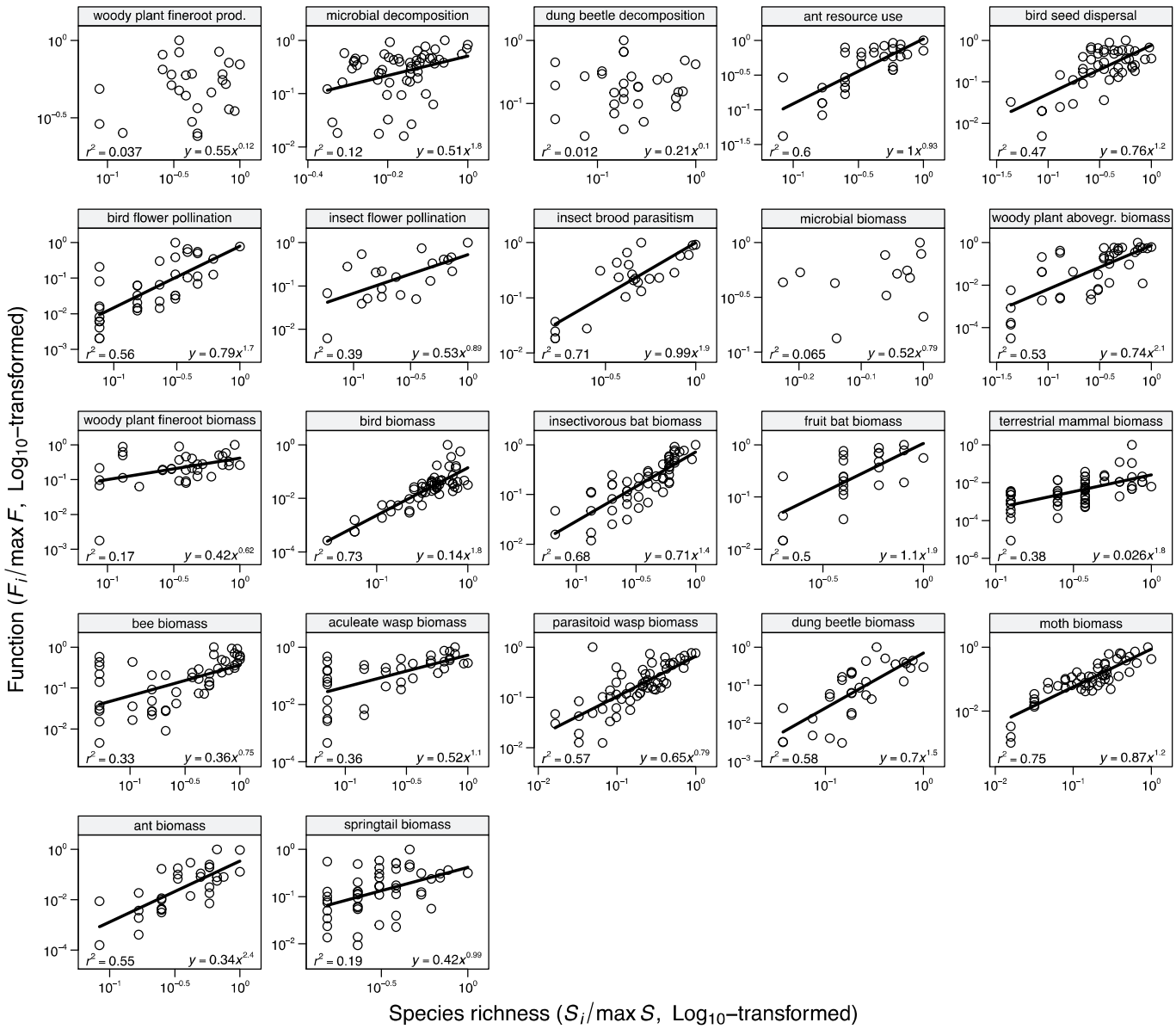


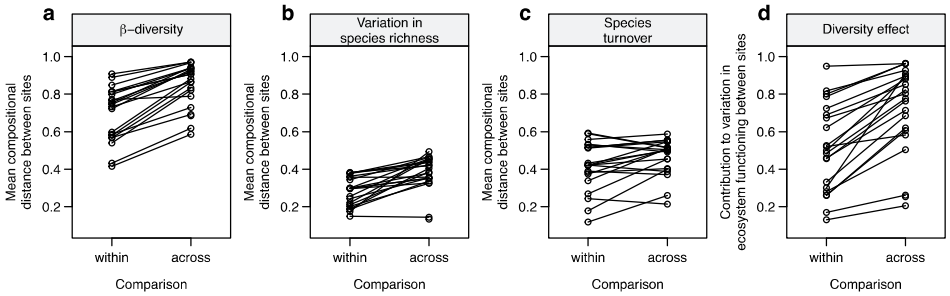
Extended Data Fig. 1 | The environmental gradients covered by the 71 study sites on Mt Kilimanjaro, Tanzania. a, Elevational distribution of the six near natural and seven anthropogenic ecosystem types. **b**, Variation in mean annual temperature (MAT, °C) and annual precipitation (MAP, mm yr^{-1}) along the elevational gradient.

	Site-level			Ecosystem-level			Mountain-level		
Function	n_{site}	S_{site}	SC_{site}	n_{eco}	S_{eco}	SC_{eco}	n_{tot}	S_{tot}	SC_{tot}
a Process rates									
Woody plant fineroot production	627	11	0.999	2037	23	1.000	16294	129	1.000
Microbial decomposition	101591	3599	0.990	465623	6905	0.997	5587480	15732	1.000
Dung beetle decomposition	40	8	0.835	151	18	0.923	1207	85	0.981
Ant resource use	410	5	0.985	1876	15	0.997	13133	74	0.999
Bird seed dispersal	200	9	0.984	919	20	0.995	9194	86	0.999
Bird flower pollination	82	3	0.994	284	6	0.997	3124	28	0.999
Insect flower pollination	202	17	0.936	353	24	0.936	4233	185	0.984
Insect brood parasitism	182	11	0.972	871	28	0.994	4356	78	0.996
b Biomass stocks									
Microbial biomass	106025	3660	0.991	106025	3660	0.991	1272297	11646	0.999
Woody plant aboveground biomass	467	9	0.999	1917	20	1.000	19165	136	1.000
Woody plant fineroots biomass	539	10	0.999	2097	21	1.000	18870	132	1.000
Bird biomass	160	15	0.969	789	34	0.988	9462	185	0.997
Insectivorous bat biomass	38	7	0.916	173	9	0.989	2077	19	1.000
Fruit bat biomass	25	2	0.971	118	4	0.995	590	6	1.000
Terrestrial mammal biomass	27	3	0.932	124	8	0.978	1606	34	0.998
Bee biomass	91	8	0.872	404	18	0.952	4843	122	0.989
Aculeate wasp biomass	7	5	0.646	26	14	0.574	282	119	0.720
Parasitoid wasp biomass	25	16	0.491	127	60	0.673	1521	517	0.782
Dung beetle biomass	40	8	0.835	160	19	0.922	1277	87	0.981
Moth biomass	33	15	0.579	147	50	0.727	1766	369	0.895
Ant biomass	410	5	0.985	1876	15	0.997	13133	74	0.999
Springtail biomass	85	5	0.967	415	9	0.995	4154	28	0.999

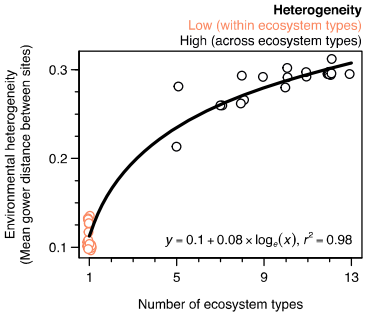
Extended Data Fig. 2 | Taxonomic sampling completeness for the 22 ecosystem functions related to process rates and biomass stocks at different sampling grains. For each function we provide the mean number of individuals sampled across sites (n_{site}), ecosystem types (n_{eco}) and the total number of individuals (n_{tot}) sampled across the elevational gradient; the mean observed species richness across sites (S_{site}), ecosystem types (S_{eco}) and the total observed species richness across the elevational gradient (S_{tot}); as well as the mean sample coverage (proportion of expected taxa sampled) across sites (SC_{site}), ecosystem types (SC_{eco}) and the total sample coverage across the elevational gradient (SC_{tot}). The sample coverage estimator quantifies the proportion of the total number of individuals in a community that belong to the species represented in the sample. The intensity of the green colour scale for sample coverage reflects sampling completeness with more intense colours indicating higher sampling completeness.



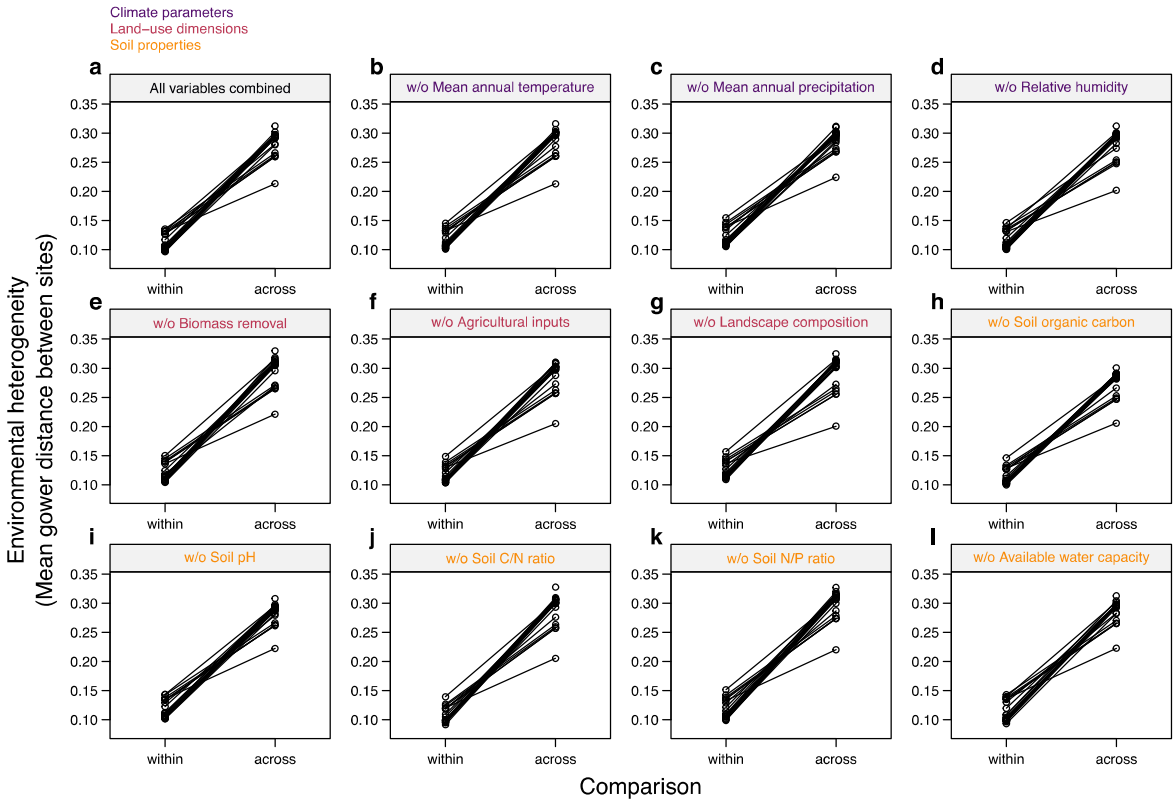
Extended Data Fig. 3 | Species richness–ecosystem function relationships across the 22 functions. All relationships are shown on log–log scales. Regression lines are shown when the relationship is significant at $P < 0.05$. Note the standardization of values of species richness and ecosystem functions by their observed maxima.



Extended Data Fig. 4 | Comparison of β-diversity and its components, as well as the diversity effect within and across ecosystem types. a-c, Comparison of (**a**) total β-diversity, (**b**) variation in species richness and (**c**) species turnover between sites within the same ecosystem types, as well as between sites across ecosystem types. **d**, Comparison of the contribution of diversity to variation in ecosystem functioning between study sites within and across ecosystem types. Each pair of dots represents the measures within and across ecosystem types for one of the 22 ecosystem functions. Note that the within-ecosystem comparison for biomass stocks of microorganisms is missing, because data were only available for one replicate per ecosystem type.



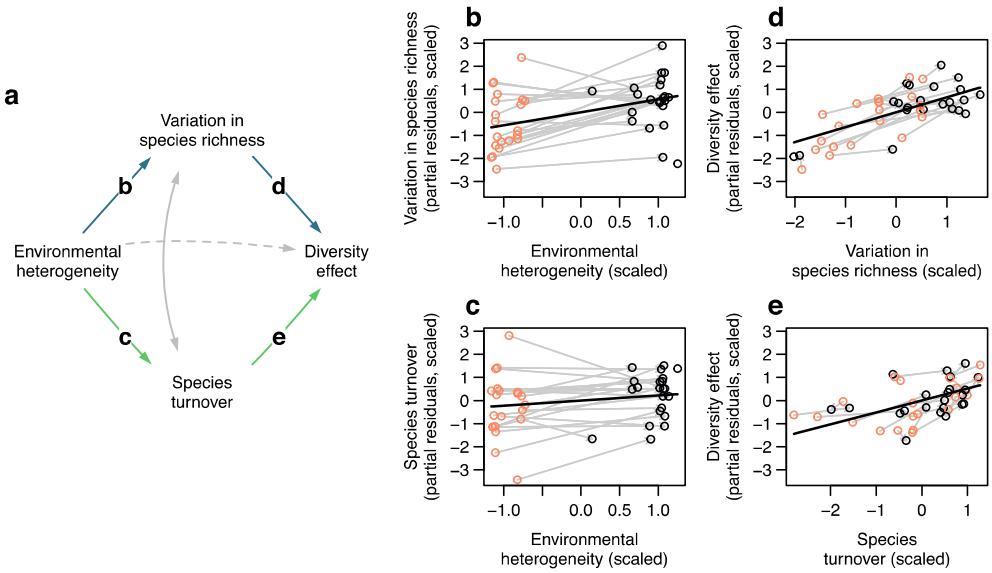
Extended Data Fig. 5 | Relationship between the number of ecosystem types and environmental heterogeneity across the 22 ecosystem functions. Shown is the mean environmental distance between study sites as a function of the number of ecosystem types. The mean environmental distance was computed based on the Gower distance on the basis of a combination of 11 variables related to climatic conditions (mean annual temperature, mean annual precipitation and relative humidity), land-use (biomass removal, agricultural inputs and landscape composition), and soil properties (soil organic carbon, pH, C/N-ratio, N/P-ratio, available water capacity). Note that noise has been added to the positions of single data points along the *x*-axis to improve visibility. Sample size is $n = 43$ ($n = 21$ within and $n = 22$ across ecosystem types, respectively).



Extended Data Fig. 6 | Comparison of environmental heterogeneity within and across ecosystem types. a–l, Comparison of the mean environmental distance (based on the Gower distance) between study sites within the same ecosystem types and between study sites across ecosystem types based on (**a**) a combination of all 11 environmental variables, and (**b–l**) after excluding each of the 11 environmental variables from the composite index of environmental heterogeneity. **b–d**, variables reflecting climate parameters. **e–g**, variables reflecting land-use dimensions. **h–l**, variables reflecting soil properties. Each pair of dots represents the measures within and across ecosystem types for one of the 22 ecosystem functions. Note that the within-ecosystem comparison for biomass stocks of microorganisms is missing, because data were only available for one replicate per ecosystem type.

Source of variance	Effect size					P_{post}	P_{prior}	$2\log_eBF$	N_{eff}	PSRF
	Median	2.5%	25%	75%	97.5%					
a Model summary										
Richness ~										
Intercept	0.33	0.29	0.32	0.34	0.36	–	–	–	10040	1.00
Heterogeneity	**0.62**	**0.39**	**0.55**	**0.7**	**0.87**	**0.9994**	**0.5**	**15**	**9881**	**1.00**
σ_f^2	0.5	0.13	0.36	0.68	1.2	–	–	–	10080	1.00
σ_ε^2	0.36	0.19	0.29	0.45	0.74	–	–	–	10220	1.00
r_m^2	0.27	0.11	0.21	0.32	0.44	–	–	–	10420	1.00
r_c^2	0.71	0.37	0.62	0.77	0.86	–	–	–	10110	1.00
Turnover ~										
Intercept	0.44	0.4	0.43	0.46	0.49	–	–	–	10430	1.00
Heterogeneity	**0.29**	**0**	**0.19**	**0.37**	**0.53**	**0.8551**	**0.5**	**3.6**	**10130**	**1.00**
σ_f^2	0.69	0.33	0.54	0.89	1.5	–	–	–	10330	1.00
σ_ε^2	0.31	0.17	0.25	0.39	0.61	–	–	–	10420	1.00
r_m^2	0.045	5.4E-35	0.019	0.076	0.15	–	–	–	10950	1.00
r_c^2	0.71	0.44	0.64	0.78	0.86	–	–	–	10280	1.00
Diversity effect ~										
Intercept	0.62	0.56	0.6	0.64	0.67	–	–	–	10280	1.00
Heterogeneity	0	-0.41	0	0	0.016	0.1595	0.5	-3.3	10110	1.00
Richness	**1.7**	**1.4**	**1.6**	**1.8**	**2.1**	**0.9994**	**0.5**	**15**	**10340**	**1.00**
Turnover	**1.1**	**0.79**	**1**	**1.2**	**1.5**	**0.9992**	**0.5**	**14**	**9900**	**1.00**
σ_f^2	0.22	0.1	0.17	0.28	0.48	–	–	–	10190	1.00
σ_ε^2	0.06	0.033	0.048	0.075	0.13	–	–	–	10400	1.00
r_m^2	0.7	0.53	0.65	0.74	0.8	–	–	–	9783	1.00
r_c^2	0.94	0.87	0.92	0.95	0.97	–	–	–	10320	1.00
Turnover ~~ Richness	-0.21	-0.45	-0.28	-0.16	-0.083	–	–	–	9942	1.00
σ_β^2	0.37	0.1	0.22	0.64	2.3	–	–	–	10000	1.05
b Direct, indirect & total effects										
Heterogeneity										
Total effect	**1.3**	**0.96**	**1.2**	**1.4**	**1.7**	**0.9996**	**0.719**	**14**	**9902**	**1.00**
Richness-mediated	**1**	**0.63**	**0.89**	**1.2**	**1.5**	**0.9992**	**0.25**	**16**	**10760**	**1.00**
Turnover-mediated	**0.32**	**0**	**0.2**	**0.42**	**0.64**	**0.8549**	**0.25**	**5.7**	**9942**	**1.00**
Direct effect	0	-0.41	0	0	0.016	0.1595	0.5	-3.3	10110	1.00
contrast: richness vs. turnover-mediated	**0.72**	**0.093**	**0.5**	**0.98**	**1.5**	**0.9862**	**0.5**	**8.5**	**10870**	**1.00**
contrast: richness vs. turnover	**0.55**	**0.13**	**0.4**	**0.69**	**1**	**0.9967**	**0.5**	**11**	**10270**	**1.00**

Extended Data Fig. 7 | Summary of Bayesian hierarchical structural equation model. The structural equation model tested for direct effects of environmental heterogeneity on the contribution of diversity to variation in ecosystem functioning (that is, the diversity effect), as well as for indirect effects that were mediated by variation in species richness and species turnover. **a**, Pairs of predictor and response variables ($y \sim x$); variance explained by the random factor for ecosystem function id (σ_f^2); residual variance (σ_ε^2) and residual covariance (Turnover ~~ Richness); variance for the path coefficients (σ_β^2); marginal variance explained by fixed effects (r_m^2); conditional variance explained by fixed and random effects combined (r_c^2). **b**, The direct, indirect and total effects of environmental heterogeneity on the diversity effect, as well as contrasts between richness- and turnover-mediated effects of environmental heterogeneity and effects of variation in species richness and species turnover. **a**,**b** Given are median effect sizes (with shrinkage), as well as the 50% and 95% credible intervals (CrIs), the posterior selection probability (P_{post}), the prior selection probability (P_{prior}), $2\log_eBF$ as a measure of support for a given effect, the effective sample size (N_{eff}) and the potential scale reduction factor (PSRF). Values of PSRF < 1.1 indicate that MCMC chains have converged on the same posterior distribution. N_{eff} indicates approximate sample size of posterior samples after accounting for temporal autocorrelation between posterior samples. Values of $2\log_eBF < 2$ indicate no support; values between 2 and 6 indicate positive support; values between 6 and 10 indicate strong support; and values >10 indicate decisive support. Effects that were supported by the variable selection with $2\log_eBF > 2$ are highlighted in bold. Sample size is $n = 43$ ($n = 21$ within and $n = 22$ across ecosystem types, respectively).

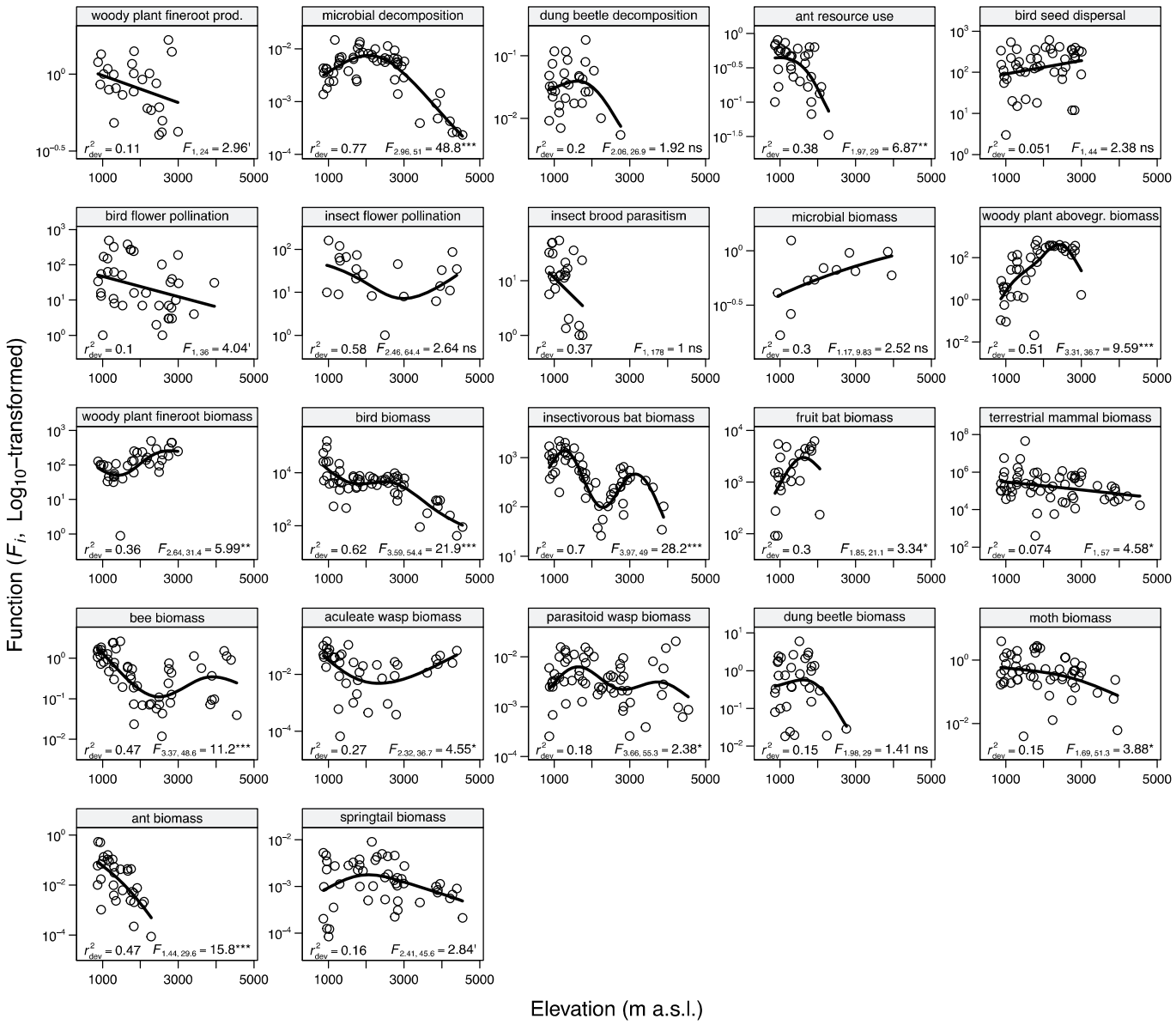


Extended Data Fig. 8 | Partial residual plots of the indirect species richness- and species turnover-mediated effects of environmental heterogeneity on the contribution of diversity to variation in ecosystem functioning. a, Topology of the Bayesian hierarchical structural equation model with the strongest support. Solid paths were supported by the Bayesian variable selection, whereas dotted paths were not (see Extended Data Fig. 7). Plots **b–e** visualize partial relationships indicated by the bold letters of the structural equation model in (**a**). Relationships of (**b**) variation in species richness and (**c**) species turnover with environmental heterogeneity. Relationships of the diversity effect with (**d**) variation in species richness and (**e**) species turnover. All variables were scaled to zero mean and unit variance before analysis. Units on the *y*-axes are standardized residual deviations from predicted partial scores after conditioning on all predictor variables except for the one shown on the *x*-axis and after conditioning on the random effects (function ID, $n_{function} = 22$). The colors of the circles represent the two types of comparisons (orange, within ecosystem types; black, across ecosystem types). The grey arrows indicate the directional change in the predictor and response variable with increasing environmental heterogeneity (that is, from comparisons within to comparisons across ecosystem types). The black lines depict the partial regression slopes. Sample size is $n = 43$ ($n = 21$ within and $n = 22$ across ecosystem types, respectively). Note that the within-ecosystem comparison for biomass stocks of microorganisms is missing, because data were only available for one replicate per ecosystem type.

Pathway	Full data		Outliers excluded		Only direct estimates	
	Effect size	$2\log_e$BF	Effect size	$2\log_e$BF	Effect size	$2\log_e$BF
Environmental heterogeneity						
Total effect: $\theta_{H\to Y} + \theta_{H\to R\to Y} + \theta_{H\to T\to Y}$	1.3 (0.96, 1.7)	14	1.3 (0.93, 1.6)	14	1.3 (0.85, 1.7)	14
Direct effect: $\theta_{H\to Y}$	0 (-0.41, 0.016)	-3.3	0 (-0.11, 0.2)	-4	0 (-0.29, 0.21)	-3.7
Effect via variation in species richness: $\theta_{H\to R\to Y}$	1 (0.63, 1.5)	16	0.97 (0.58, 1.4)	16	1.1 (0.66, 1.6)	16
Effect via species turnover: $\theta_{H\to T\to Y}$	0.32 (0, 0.64)	5.7	0.3 (0, 0.58)	6.3	0.13 (0, 0.61)	2.7
Contrast of indeirect effects: $\theta_{H\to R\to Y}$ versus $\theta_{H\to T\to Y}$	0.72 (0.093, 1.5)	8.5	0.66 (0.077, 1.4)	8.5	0.95 (0.17, 1.6)	11
β-diversity components						
Variation in species richness: $\theta_{R\to Y}$	1.7 (1.4, 2.1)	15	1.6 (1.3, 1.9)	15	1.6 (1.2, 2)	15
Species turnover: $\theta_{T\to Y}$	1.1 (0.79, 1.5)	14	0.97 (0.68, 1.2)	14	1.2 (0.78, 1.5)	14
Contrast of direct effects: $\theta_{R\to Y}$ *versus* $\theta_{T\to Y}$	0.55 (0.13, 1)	11	0.63 (0.26, 1)	17	0.4 (-0.1, 0.94)	5.7

Pathway	Natural ecosystems		Anthropogenic ecosystems		Detrended data	
	Effect size	$2\log_e$BF	Effect size	$2\log_e$BF	Effect size	$2\log_e$BF
Environmental heterogeneity						
Total effect: $\theta_{H\to Y} + \theta_{H\to R\to Y} + \theta_{H\to T\to Y}$	1.7 (1.2, 2.2)	14	1.2 (0.75, 1.6)	13	1.1 (0.78, 1.4)	14
Direct effect: $\theta_{H\to Y}$	0 (-0.21, 0.4)	-3.7	0 (-0.32, 0.075)	-3.9	0 (-0.4, 0.03)	-3.1
Effect via variation in species richness: $\theta_{H\to R\to Y}$	1.2 (0.61, 1.9)	14	1 (0.43, 1.5)	12	0.82 (0.49, 1.3)	16
Effect via species turnover: $\theta_{H\to T\to Y}$	0.49 (0, 0.96)	6.2	0.073 (0, 0.66)	2.4	0.32 (0, 0.64)	5.7
Contrast of indirect effects: $\theta_{H\to R\to Y}$ versus $\theta_{H\to T\to Y}$	0.69 (-0.22, 1.8)	5.4	0.91 (-0.15, 1.5)	6	0.49 (-0.07, 1.2)	6.3
β-diversity components						
Variation in species richness: $\theta_{R\to Y}$	1.5 (1.2, 1.8)	15	1.7 (1.4, 2.2)	15	1.3 (1, 1.7)	15
Species turnover: $\theta_{T\to Y}$	1 (0.65, 1.3)	14	1.2 (0.82, 1.6)	14	1.1 (0.82, 1.5)	14
Contrast of direct effects: $\theta_{R\to Y}$ *versus* $\theta_{T\to Y}$	0.52 (0.078, 0.96)	9.2	0.54 (0.058, 1.1)	8.6	0.19 (-0.2, 0.62)	3.2

Extended Data Fig. 9 | Summary of sensitivity analysis. Shown are effect sizes θ estimated by the Bayesian hierarchical structural equation model (medians and 95% credible intervals (CrIs) based on the posterior distribution of estimated model parameters) for several subsets of the data and for several treatments of the data prior to analyses; $2\log_e$BF ($2\log_e$[Bayes Factor]) as a measure of evidence for a given effect. Effect sizes reflect the expected change in the response variable for a 1% change in the predictor variable (for example, $\theta_{R\to Y}=1.7$ means that an increase of 10% in variation in species richness causes an increase of 17% in the diversity effect). Values of $2\log_e$BF < 2 indicate no support; values between 2 and 6 indicate positive support; values between 6 and 10 indicate strong support; and values >10 indicate decisive support.



Extended Data Fig. 10 | Relationships between elevation and ecosystem functioning across the 22 functions. Regression lines represent best-fit generalized additive models with a thin plate spline (second-order penalty of $m = 2$ and basis dimension of $k = 5$ if $n > 40$ and $k = 4$ otherwise). Note the log-scale on the *y*-axes. r^2_{dev}, proportion of deviance explained by the model. ns, $P > 0.1$;'$P < 0.1$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. Subscripts of *F*-values indicate the effective degrees of freedom of the smooth term and the residual degrees of freedom.

nature portfolio

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Last updated by author(s): Aug 3, 2021

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For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed
☐	☒ The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒ The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒ A description of all covariates tested
☐	☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
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☐	☒ For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☐	☒ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒ Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Original data was downloaded as csv files with permission of data owners via the KiLi data base or send by personal emails. All data was originally stored as csv files (handled with Microsoft Excel version 16.45) and imported into R (version 4.0.3) using R Studio (version 1.3.1093) programme.
Data analysis	All data analyses was conducted in R (version 4.0.3) via R Studio (version 1.3.1093) and the following R packages: coda (0.19-4), iNEXT (2.0.20), LaplacesDemon (16.1.4), mgcv (1.8-33), parallel (4.0.3), qgraph (1.6.5), rjags(4-10), vegan (2.5-7), viridis (0.5.1). The code used for the analysis is deposited in figshare with the identifier https://doi.org/10.6084/m9.figshare.14544207.

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Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

The data that support the findings of this study are deposited in figshare with the identifier https://doi.org/10.6084/m9.figshare.14544207.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	In the present study, we assess how environmental heterogeneity shapes the effect of diversity on ecosystem functioning and to what extent this diversity effect is mediated by variation in species richness or species turnover in a non-experimental system. For this purpose, we introduce a novel framework that allows to quantify the variation in ecosystem functioning resulting from variation in species richness and species turnover (the two fundamental components of β-diversity). First, we quantified the contribution of diversity in terms of variation in species richness (quantitative variable) and species turnover (quantitative) to variation in 22 ecosystem functions (all quantitative) of microorganisms, plants and animals across 13 ecosystem types along a 3.7 km elevation gradient on Mt. Kilimanjaro. Then we used a Bayesian hierarchical structural equation model with a stochastic variable selection procedure to quantify the direct effect of environmental heterogeneity on the contribution of diversity to variation in ecosystem functioning, as well as the indirect effects that were mediated by variation in species richness and species turnover.
Research sample	The data were collected on a total of 71 study sites that were distributed across the entire elevational gradient of Mt. Kilimanjaro. However, the sample size for individual ecosystem functions varied between 12 and 60, because not all functions could be measured on all study sites (e.g., because some taxonomic groups did not occur along the entire elevational gradient). As all study sites were geographically seperated by a distance of at least 300 m and 97% of all pairs of study sites were seperated by more than 2 km we considered study sites as independent replicates. For two ecosystem functions (insect brood parasitism and insect pollination) repeated measures were taken on the study sites. For these functions we first calculated the focal metrics for each observation and then calculated a mean value per study site for all further analyses. The procedure is also described in the methods section of the paper. The exact sample size is indicated for each ecosystem function in Fig. 2 of the paper.
Sampling strategy	The number of study sites represents a balance between good statistical power and feasibility. The number of study sites was not chosen with a single specific variable in mind (as we targeted in total 22 ecosystem functions) but based on our experience in the analyses of ecological data.
Data collection	The data was collected between 2011 and 2016 on the 71 research study sites established by the KiLi project using specific methods for plants, different groups of animals, microbes and 22 ecosystem functions. A.H. established study sites. C. Bogner, K.B.-G., R.B., M.F., A.H., D.H., B.H., R.K., M.K., Y.K., C.L., T.N., M.K.P., M.S., I.S.-D. and M.T. conceptualised and supervised data collection. J.N.B., C. Behler, A.C., H.I.D., C.D.E., A.E., S.W.F., F. Gebert, F. Gerschlauer, M.H.-B., A.H., V.K., A. Keller, W.J.K., A. Kühnel, A.V.M., H.K.N., H.P., M.K.P., R.S.P., U.P., J.R., G.R., D.S.C., N.S.-C., A.V., M.G.R.V. and J.Z. collected data. A.H., C.H., H.I.D, K.M.H., V.K. and J.Z. supported data collection and field work.
Timing and spatial scale	All data were collected from January 2011 through December 2016 on the southern and south-eastern slopes of Mt. Kilimanjaro (Tanzania, East Africa; 2°45'-3°25'S, 37°00'-37°43'E). Depending on the variable, data on study sites was collected few (e.g. most data sets on community composition and ecosystem functions) to hundreds of times (e.g. climate data). Detailed collection protocols for each variable are described in the methods section of the paper.
Data exclusions	No data was excluded.
Reproducibility	As this was not a true experiment but an observational study in a real ecosystem, the study could not be truly repeated. If feasible, most variables were taken multiple times per study site in order to achieve a high precision. The data and code to reproduce the analysis is publicly available in figshare with the identifier https://doi.org/10.6084/m9.figshare.14544207.
Randomization	We think that this point applies more to a true experiment, while we describe and analyse ecological data from a real mountain ecosystem where covariates are necessarily partly correlated. We dealt with this by applying several sensitivity analyses (i.e., excluding ecosystem functions for which only indirect estimates of species-specific functional contributions were available, excluding study sites with extreme data values, analyzing subsets of the data from natural and anthropogenic ecosystems, analyzing the data after removing potential effects of environmental covariates). All of these sensitivity analyses led to the same conclusions.
Blinding	See above. This was a study in a real mountain ecosystem but not a true experiment. The data was sampled by the coauthors without the specific hypotheses of the present study in mind, which, in our view, generates a comparative "blinding effect".

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	The study was conducted along the southern and south-eastern slopes of Mt. Kilimanjaro across an elevational gradient from the lowlands (ca. 850 m a.s.l.) to the highest point with vegetation (4550 m a.s.l.). Across the elevational gradient mean annual temperature ranges from 25°C at the foothills and 2.9°C at the point where the highest study site is located. Mean annual precipitation is unimodally distributed with a peak at 2200 m asl (ca. 2550 mm) and lowest values in the lowlands (ca. 600 mm). A

	figure that summarizes the environmental conditions is provided as Extended Data (Extended Data Fig. 1). Moreover, additional details are provided in the Methods section of the paper.
Location	The study area is located on the southern and south-eastern slopes of Mt. Kilimanjaro (Tanzania, East Africa; 2°45'-3°25'S, 37°00'-37°43'E). We worked on a total of 71 study sites, which spanned an elevational gradient from ca. 850 to 4550 m a.s.l.
Access & import/export	We studied biodiversity and ecosystem functions in all major ecosystem types of the study region. Research was conducted together with our counterparts (of which many are coauthors) in full compliance with local, national and international laws. Permits for field work and export of samples were issued to all data collectors by the Tanzania Commission for Science and Technology (COSTECH) and the Tanzania Wildlife Research Institute (TAWIRI) under the following permit numbers: COSTECH, TAWIRI: 2010-241-NA-96-44, 2010-239-ER-96-44, 2010-356-NA-96-44 to 2010-368-NA-96-44, 2011-311-ER-96-44, 2011-310-ER-96-44, 2011-337-NA-96-44-to 2011-350-ER-96-44, 2012-417-ER-96-44, 2012-416-ER-96-44 2012-468-ER-96-44 to 2012-469-ER-96-44, 2013-310-ER-96-44 to 2013-323-ER-96-44, 2014-329-NA-96-44, 2014-331-NA-96-44, 2014-295-NA-96-44 to 2014-300-NA-96-44, 2014-303-ER-96-44 to 2014-313-NA-96-44, 2015-178-NA-96-44, 2015-178-NA-96-44, 2015-174-NA-96-44 to 2015-178-NA-96-44, 2016-100-ER-96-44, 2016-102-ER-96-44, TNP/HQ/C.10/13.
Disturbance	As we aimed at collecting data in unmanipulated ecosystems, we did not experimentally modify any vegetation. Vertebrates were sampled by acoustic and visual detection, to minimize any disturbance of wildlife. To assess biodiversity of arthropods we had to collect, kill and preserve them. However, we are confident that this did not have a major impact on the species populations.

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Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	No laboratory animals were used.
Wild animals	During the study we recorded mammals, birds and arthropods. Mammals and birds were identified by visual and acoustic detection; they were neither captured nor killed. Arthropods were collected using ethanol or ethylenglycol for killing and preservation of specimens. Arthropods were mounted and labelled to be stored in public museum collections in Germany and Tanzania.
Field-collected samples	Field samples taken on Mt. Kilimanjaro were stored in ethanol (nearly all arthropod samples), Xpedition sample processor (microbes; Zymo Research Corporation, Irvine, CA, USA), pressed and dried (plants) before further processing in the laboratory.
Ethics oversight	No ethical approval was necessary. Vertebrates were sampled by acoustic and visual detection, to minimize any disturbance of wildlife. Furthermore, we did not collect protected or threatened arthropod species and did not conduct any experiments with animals.

Note that full information on the approval of the study protocol must also be provided in the manuscript.