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Functional diversity and redundancy of tropical forests shift with elevation and forest-use intensity

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Abstract

1. Change and intensification of forest use alter tropical ecosystems, influencing biodiversity and, subsequently, ecosystem functioning. The implications of eroding biodiversity may go beyond decreases in species diversity, resulting in changes of functional diversity, i.e. the diversity of ecological strategies present in the community, and functional redundancy, i.e. how redundant these strategies are to biodiversity loss. However, how environmental conditions and anthropogenic influences shape functional diversity and redundancy in tropical forests remains poorly understood.
2. Here, we examine how tropical forests respond to forest-use intensity along an extensive elevational gradient in Mexico from the tropical lowlands to high-elevational mountain forests (0 to 3500 m), in terms of functional diversity and functional redundancy, and how these biodiversity facets are related to forest structure. In our study, elevation was crossed with three levels of forest-use intensity: old-growth, degraded, and secondary forests. At eight elevational sites, five replicate plots were inventoried for each level of forest-use intensity (total n = 120 plots). Functional diversity and redundancy were calculated using leaf and wood traits of 144 tree species for Hill numbers zero, one, and two.
3. Interactive effects between elevation and forest-use intensity significantly affected biodiversity facets. However, interactive effects resulted from forest-use intensity influencing biodiversity facets at only a few elevations, and not from a consistent, negative impact of forest-use intensity. Forest structure, specifically stem density and the Gini coefficient, explained variation across biodiversity facets when these facets gave equal weight to common and rare species.
4. Synthesis and applications. High functional diversity and functional redundancy from lowland to mid-elevation tropical forests suggest that these ecosystems can be resilient to future disturbances. Our results indicate that the ability of high-elevation forests may be particularly susceptible to climate change and increasing forest-use intensity. For these high-elevation

forests, we recommend that forest managers implement enrichment plantings with native species that can tolerate future environmental conditions. Finally, our study shows that efforts to conserve structurally heterogeneous forests and actively managing forests to increase structural heterogeneity will enhance the resilience of tropical forests while conserving their biodiversity.

Keywords: Degraded forest, Elevational gradient, Forest structure, Functional traits, Land-use, Old-growth forest, Secondary forest, Tropical forests

Resumen

1. El cambio y la intensificación del uso del bosque altera los ecosistemas tropicales, influenciando la biodiversidad y subsecuentemente, el funcionamiento del ecosistema. Las consecuencias de pérdidas de la biodiversidad podrían ir más allá de la reducción de la diversidad de especies, resultando en cambios de la diversidad funcional – en otras palabras, la diversidad de estrategias ecológicas presentes en la comunidad – y la redundancia funcional, es decir que tan redundantes son estas estrategias a la pérdida de la diversidad. Sin embargo, como las condiciones ambientales y las influencias antropogénicas determinan la diversidad y redundancia funcional en los bosques tropicales, se entiende escasamente.
2. Aquí, nosotros examinamos cómo la diversidad y redundancia funcional de los bosques tropicales responden a la intensidad de uso forestal a lo largo de un amplio gradiente

elevacional en México – cubriendo desde las tierras bajas tropicales hasta los bosques de alta montaña (0 a 3500 m) – y como estas facetas de la biodiversidad están relacionadas con la estructura del bosque. En nuestro estudio, la elevación se cruzó con tres niveles de intensidad de uso forestal: bosque maduro, bosque degradado y bosque secundario. En ocho pisos elevacionales, se inventariaron cinco parcelas por cada nivel de intensidad de uso forestal (total n=120 parcelas). La diversidad y la redundancia funcionales fueron calculadas usando rasgos funcionales de hojas y de madera de 144 especies de árboles para los números Hill cero, uno, y dos.

3. Los efectos interactivos entre la elevación y la intensidad de uso forestal afectaron significativamente las facetas de biodiversidad. Sin embargo, estos efectos interactivos se debieron a que la intensidad de uso forestal influyó las facetas de biodiversidad en pocas elevaciones, en vez de un impacto negativo consistente de la intensidad de uso forestal. La estructura del bosque, específicamente la densidad de tallos y el coeficiente de Gini, explicó la variación de las diferentes facetas de biodiversidad cuando estas facetas daban igual peso a especies comunes y raras.
4. Síntesis y aplicaciones. La alta diversidad y redundancia funcional de los bosques tropicales ubicados entre tierras bajas hasta elevaciones medias sugiere que estos ecosistemas pueden ser resilientes contra disturbios en el futuro. Por el contrario, nuestros resultados indican que la capacidad de los bosques en altas elevaciones puede ser particularmente susceptibles al cambio climático y al incremento del uso forestal. Por ende, nosotros recomendamos la implementación de enriquecimiento forestal en bosques en altas elevaciones con especies nativas que puedan tolerar las condiciones ambientales futuras. Finalmente, nuestro estudio demuestra que los esfuerzos para conservar bosques heterogéneos estructuralmente y la gestión activa para aumentar la heterogeneidad estructural de los bosques mejorará la resiliencia de los bosques tropicales conservando al mismo tiempo su biodiversidad.

Palabras claves: Bosque degradado, Bosque maduro, Bosque secundario, Bosques tropicales, Estructura del bosque, Gradiente elevacional, Rasgos funcionales, Uso del suelo

Introduction

Human activities are causing alarming losses of biodiversity and alter ecosystem functioning worldwide (Díaz et al., 2019), and this loss is most pronounced in the tropics where high biodiversity and high human impacts coincide. The implications of eroding biodiversity go beyond simple decreases in species diversity, also resulting in changes in the range or dispersion of traits of the organisms present in a community, i.e. functional diversity (Díaz & Cabido, 2001; Maire et al., 2015) and the extent to which species perform similar functions, i.e. functional redundancy (Ricotta et al., 2016). This means that functional diversity encompasses the diversity of ecological strategies present in a community, while functional redundancy reveals the potential impacts on ecosystem functioning due to species losses, i.e. how redundant these strategies are. Consequently, human impacts on functional diversity and redundancy may influence the provisioning of ecosystem functions and may determine the resilience, i.e. the capacity of a forest to return to the state before a disturbance, of ecological communities to multiple global change drivers, particularly land-use change and intensity (Jakovac et al., 2015; Payne et al., 2017; Peters et al., 2019). However, the impacts of forest-use intensity on functional diversity and redundancy are variable (Carreño-Rocabado et al., 2012; Laliberté et al., 2010) and could be intensified or mitigated by environmental conditions (Peters et al., 2019).

Tropical mountains are natural laboratories to study responses of plant diversity, community composition, and ecosystem functioning in relation to elevation and environmental conditions (Körner et al., 2017). Plant species diversity (specifically, species richness) along elevation is expected to be driven by the availability of ambient energy (e.g. temperature, potential evapotranspiration) and water (Kreft & Jetz, 2007) that combine to drive differences in productivity. Yet, plant species diversity along elevational gradients also may be related to the number of individuals (more individuals hypothesis; MIH) (Storch et al., 2018; Wright, 1983). Consequently, higher elevations with lower energy availability are expected to have lower diversity, smaller tree

populations, and less biomass than lower, warmer elevations (e.g. Givnish, 1999). While there is growing evidence that functional diversity may respond similarly along elevational gradients as species diversity (e.g. Durán et al., 2019; Luo et al., 2019; Thakur & Chawla, 2019), how functional redundancy may shift with elevation is uncertain. By limiting the number of viable phenotypes, e.g. combinations of trait values, that respond to elevation and forest-use intensity (Bello et al., 2013; Dainese et al., 2015; Wieczynski et al., 2019), environmental filtering increases the possibility that co-occurring species perform similar functions. For example, functional redundancy may be higher in harsh environments, where high aridity or low temperatures reduce the number of viable ecological strategies. In areas with more favorable environmental conditions (e.g. high precipitation and warm temperatures), which permit the coexistence of a greater number of species with contrasting ecological strategies, functional redundancy may be either high or low as multiple ecological strategies may be represented by many species (high redundancy) or by few species (low redundancy) (Bello et al., 2013). Expected patterns of functional diversity and redundancy along elevational gradients, however, are likely impacted by forest-use intensity, either directly or indirectly through shifts in forest structure.

Forest-use intensity, e.g. in the form of timber extraction or cattle grazing, is one of the main drivers modifying the structure, i.e. the distribution of biomass, characterized by stem density, basal area, canopy cover, or height (Goff & Zedler, 1968), vertical and horizontal components of heterogeneity (Schall et al., 2018), and biodiversity of tropical forest ecosystems (Peters et al., 2019). For instance, high forest-use intensity may reduce tree biomass and stem density (Ensslin et al., 2015; Muller-Landau et al., 2021; Whitfeld et al., 2014), while intermediate forest-use intensity may increase biomass (Marín-Spiotta et al., 2007). Similarly, high intensity forest-use often simplifies forest structure by homogenizing the age and size distribution of trees (Schall et al., 2018; Zemp et al., 2019), leading to fewer niches and, therefore, lower diversity (Heidrich et al., 2020; Stein et al., 2014). The resulting mosaic in forest structure across human-impacted tropical ecosystems usually leads to positive relationships between forest structure and functional diversity (Craven et al., 2016;

Lohbeck et al., 2012). However, *direct* responses of functional diversity and redundancy to land-use type and intensity in tropical forests are quite variable, as management practices may introduce new species that bring in new trait combinations or mix species from different habitats (Carreño-Rocabado et al., 2012, 2016; Laliberté et al., 2010). Moreover, the effects of forest-use intensity on biodiversity may be *indirect*, operating via landscape configuration (Jakovac et al., 2015) or habitat loss (Chase et al., 2020). The impacts of forest-use intensity on biodiversity may be further intensified or dampened by underlying environmental conditions (Guzmán-Jacob et al., 2020; Monge-González et al., 2020). A comprehensive study from Mount Kilimanjaro showed that interactions between climate and forest-use intensity had stronger effects on species diversity and ecosystem functioning than individual drivers (Peters et al., 2019). However, the impacts of environmental conditions, forest structure, and forest-use intensity - and their interactions - on functional diversity and redundancy, to our knowledge, have yet to be examined in tropical forests.

Here, we investigate how tropical forests respond to forest-use intensity along an elevational gradient, in terms of their potential to provide ecosystem functions (i.e. functional diversity) and their ability to recover from biodiversity losses (i.e. functional redundancy) and how functional diversity and redundancy are related to forest structure. We expect that environmental conditions, here captured by the extensive elevational gradient, and forest structure jointly mediate the impacts of forest-use intensity on functional diversity and redundancy in tropical forests. Specifically, we expect an overall negative influence of forest-use intensity on functional diversity and redundancy. Yet, the magnitude of the expected negative effect of forest-use intensity may vary because of environmental conditions (Peters et al., 2019), likely being greater where environmental conditions are harsher. Further, we expect that structurally complex forests with high basal area, stem density, or size heterogeneity are associated with greater functional diversity and redundancy, as they provide more resources and, therefore, more opportunities for niche partitioning. In contrast, forest-use intensity may lead to habitat simplification by reducing structural complexity, increasing the vulnerability of specific plant functional strategies. By showing how functional diversity and

redundancy shift across gradients in forest-use intensity and environmental conditions, we seek to provide recommendations for biodiversity conservation and the management of the provisioning of ecosystem functions in dynamic, human-dominated tropical landscapes. Because the impacts of forest-use intensity are likely to vary across elevations, our study will provide guidelines as to where efforts (e.g. forests at high versus low elevations, or areas with high versus low forest-use intensity) should be focused to improve the outcomes of programmes to conserve biodiversity and maintain ecosystem functioning in tropical regions.

Materials and methods

Study region

The study was conducted along an elevational gradient ranging from sea level close to the Gulf of Mexico (19.5894° N, 96.375167° W) to near tree line at 3545 m elevation (tree line in the study area at 4000 m where the dominant species is *Pinus hartwegii*; Toledo-Garibaldi, 2012) (19.5182° N, 97.154525° W) on the eastern slopes of Cofre de Perote, an extinct stratovolcano of 4282 m, in the state of Veracruz, Mexico. The flora in the study region combines elements of Nearctic and Neotropical origin, with an elevational sequence of tropical semi-humid deciduous, tropical oak, humid montane, pine-oak, pine, and fir forests (Carvajal-Hernández et al., 2020).

Study design and data collection

We selected eight sites at approximately 500 m intervals along the elevational gradient between 30 and 3545 m. In the following, we refer to each site simply as 0, 500, 1000, 1500, 2000, 2500, 3000, and 3500 m. At each site, we established 15 plots of 20 m x 20 m each, in the same vegetation type, with five replicate plots each in old-growth forest (defined here as a mature forest with low forest-use intensity and without any visible signs of recent human disturbance), degraded forest (with clear signs of human disturbance, like e.g. cattle ranching, fire wood extraction; classified as intermediate forest-use intensity), and secondary forest (15 – 20 years old regrowth after abandonment; assessed based on interviews with landowners). In total, we sampled 120 plots covering a total area of 48,000 m². On each plot, all trees with a diameter at breast height (DBH; 1.3 m) > 5 cm were measured and

identified to the lowest possible taxonomic resolution. Vouchers of specimens were deposited at the herbarium XAL of Instituto de Ecología, A. C. at Xalapa, Mexico. We also counted the number of stems, and measured DBH (cm) and tree height (m) following the protocol of Homeier et al. (2010). Details of the floristic inventories are reported in Monge-Gonzalez et al. (2020).

Functional trait sampling

We selected seven plant functional traits: maximum tree height (m), wood density (g cm^{-3}), specific leaf area ($\text{m}^2 \text{ kg}^{-1}$), leaf dry matter content (g g^{-1}), lamina density (g cm^{-2}), chlorophyll content ($\mu\text{g cm}^{-2}$), and leaf area (cm^2). We chose these traits because they capture variation in plant growth and function, are linked to ecosystem functioning, and are likely to respond to changes in forest-use intensity and climate (Díaz et al., 2016; Pérez-Harguindeguy et al., 2016). Traits were measured following standardized measurement protocols (Chave et al., 2005 for wood density; King et al., 2006 for maximum tree height; Pérez-Harguindeguy et al., 2016 for leaf traits). Because we were not able to collect traits for all species in our plots, we obtained wood density values for 44 species from the Botanical Information and Ecology Network (BIEN) database (Enquist et al., 2016). We also performed phylogenetic trait imputation for 39 species (Fig. S1) with missing leaf traits following Penone et al. (2014); for details see Supplementary Methods. We restricted our analysis to the 111 plots for which we had trait data for at least 90% of all individuals (Pakeman & Quested, 2007).

Data analysis

Species and functional diversity

For functional diversity, we calculated a functional dissimilarity matrix between all species based on the abovementioned functional traits, having first determined the number of functional dimensions that maximizes the quality of functional spaces (Fig. S2, Table S1; Maire et al., 2015). Subsequently, we used the approach by Chao et al. (2019), that overcomes the limitation of traditional indices of functional diversity (Laliberté et al., 2010) that often give similar values to communities with different levels of functional diversity. To this end, this approach uses a threshold of functional

distinctiveness (" τ ") between any two species to quantify the effective numbers of functionally equally distinct species in an assemblage (Chao et al., 2019). Here, we used two distinctiveness thresholds: d_{min} which assumes that each species is maximally distinct from other species, i.e. species diversity, and d_{mean} which is the effective number of functionally equally distinct species calculated based on the mean distance between any two species from the assemblage, i.e. interpreted as functional diversity (Chao et al., 2019). In addition, for any value of τ , diversity can be estimated for any Hill number (Fig. S3; Jost, 2006). Thus, for both species and functional diversity, i.e. d_{min} and d_{mean} , respectively, we calculated the effective number of species or functional groups irrespective of their abundance (Hill number $q = 0$, i.e. richness) and the effective number of species or functional groups weighted by the abundance of common (Hill number $q = 1$, i.e. Shannon diversity) or abundant species or functional groups (Hill number $q = 2$, i.e. Simpson diversity).

Functional redundancy

Following Ricotta et al. (2016), we estimated functional redundancy for each Hill number as the difference between species and functional diversity. Using the different Hill numbers elucidates if the ecological functions of rare, common or abundant species can be replaced by another species in the community. Thus, communities with high functional redundancy may recover from biodiversity loss because they are composed of species with similar trait values, meaning that if one species is lost, another can provide similar ecological functions. In contrast, in communities with low functional redundancy ecological functions cannot be replaced by other species in the community.

Forest structure

For each plot, we quantified four commonly used measures of forest structure, namely stem density, structural heterogeneity, stand basal area, and aboveground biomass (Supplementary Methods). We estimated stem density as the number of individuals per plot, and structural heterogeneity using the Gini coefficient of tree DBH, using the 'Gini' function in the 'ineq' package in R (Zeileis & Kleiber, 2014). We calculated basal area per plot (BA in m^2), using the following formula: $BA = (\pi \times$

DBH²)/40,000. Due to the strong correlation between stand basal area and aboveground biomass ($R = 0.83$, Fig. S4), and because basal area captures variation in forest age, successional status and species composition (Breugel et al., 2006), we used basal area in subsequent analyses.

Statistical analysis

We examined the main effects of elevation and forest-use intensity as well as their interaction, and forest structure (measured as stem density, Gini coefficient, and basal area) on species and functional diversity and redundancy for each Hill number using an analysis of variance (ANOVA) Type III implemented in the “car” package (Fox & Sanford, 2019). To assess the influence of collinearity of predictor variables in the regression models, we calculated the variance inflation factor (VIF). We used natural logarithmic transformation for functional and species diversity to meet assumptions of normality.

Similarly, we assessed the main effects of elevation, forest-use intensity as well as their interaction on forest structure and stem density using a generalized linear model with a Poisson distribution implemented in the R function ‘glm’ and on Gini coefficient and basal area using linear models. In all models, we treated forest-use intensity and elevation as factors.

For data manipulation and visualization, we used the R packages ‘dplyr’ (Wickham et al., 2019) and ‘ggplot2’ (Wickham, 2009), respectively. We performed all analyses in R version 3.6.3 (R Core Team, 2020).

Results

Relationships between facets of diversity

Functional diversity and redundancy were positively correlated with species diversity, with consistent positive relationships independent of whether rare, common, or abundant species were

considered (Fig. 1). However, the shape of the relationship varied, with functional diversity saturating, while functional redundancy linearly increasing with species diversity (Fig. 1). Specifically, we found that functional diversity was significantly positively associated with species diversity (Spearman correlation coefficients = 0.62, 0.81, and 0.86, for Hill numbers 0, 1, and 2, respectively, all p-values $<2.2 \text{ e}^{-16}$, Fig. S5). Yet, relationships between functional and species diversity saturated around five species; communities below this point had higher functional diversity than functional redundancy, while communities above this inflection point showed an inverse pattern. For functional redundancy, we found significantly positive relationships with species diversity (Spearman correlation coefficients = 0.97, 0.97, and 0.96, for Hill numbers 0, 1, and 2, respectively, all p-values $<2.2 \text{ e}^{-16}$, Fig. S5).

Influence of the interactive effects between elevation and forest-use intensity and forest structure on facets of diversity

Interactive effects between elevation and forest-use intensity explained functional diversity, redundancy, and species diversity across Hill numbers (Table 1, Figs. 2, S6 and S7). For instance, functional diversity (Hill numbers 0, 1, and 2) was explained by significant interactions between elevation and forest-use intensity (Table 1), with these interactions emerging mostly due to 1) differences among forest-use intensity at 1500 m (between old-growth and secondary forest) and 2) marginal increases in functional diversity with forest-use intensity at 1000, 3000, and 3500 m, in contrast to slight decreases or no change with forest-use intensity for the other elevations (Fig. 2). Similarly, functional redundancy and species diversity (Hill numbers 0, 1, and 2) were explained by significant interactions between elevation and forest-use intensity (Table 1), with these significant interactions mostly explained by differences in functional redundancy between old-growth and secondary forests at 0 m and among forest-use intensities at 1500 m for both functional redundancy and species diversity (Fig. 2).

Forest structure measured as stem density and Gini coefficient of DBH explained variation across biodiversity facets only when the effective number of species, functional groups, or functional redundancy were calculated irrespective of their abundances ($q = 0$, Table 1). Specifically, functional redundancy and species diversity increased significantly with stem density (Table 1, Fig. 3B and 3D), while functional and species diversity increased significantly with structural heterogeneity, i.e. Gini coefficient of DBH (Table 1, Fig. 3A and 3C). While basal area was influenced significantly by the interaction between elevation and forest-use intensity, as were stem density and Gini coefficient (Table S2, Fig. S8), it did not explain differences in any of the studied biodiversity facets (Table 1).

Discussion

Previous research provided strong evidence that elevation and forest-use intensity interactively affect species diversity (Monge-González et al., 2020; Peters et al., 2019). Our study is one of the first that assesses the interactive effects of elevation and forest-use intensity on other facets of biodiversity, while simultaneously examining the effects of forest structure. Our results revealed that functional diversity and redundancy are affected by the interaction between elevation and forest-use intensity, resulting in different elevational patterns across forest-use intensity levels. However, forest-use intensity did not affect functional diversity or redundancy at most elevations. In fact, our study revealed that from sea level to 2000 m tree communities had a high functional diversity and redundancy, making them more resilient to disturbances than tree communities at higher elevations. We found that forest structural attributes uniquely impacted all biodiversity facets for Hill number 0, suggesting that more heterogeneous forests enhanced biodiversity via its positive effects on functionally rare species.

We found that functional diversity and redundancy in old-growth forests dropped sharply above 2000 m. This mirrors patterns for tree species diversity reported in a related study by Monge-González et al. (2020), suggesting that more diverse tree communities at low and mid-elevations may be more resilient than the species-poor tree communities at higher elevations. At

higher elevations (particularly 3000 – 3500 m), lower functional diversity and redundancy may reflect strong environmental filtering (Spasojevic & Suding, 2012). Decreases in temperature with increasing elevation are known to affect changes in plant functional traits and to cause functional convergence at high, cold elevations by constraining trait variation (Durán et al., 2019; Wieczynski et al., 2019). However, the elevational patterns for functional diversity and redundancy observed in our study indicate that elevational shifts in the strength of environmental filtering are non-linear. This suggests that other environmental factors also influence functional diversity and redundancy, but may not change linearly with elevation (e.g. precipitation; McCain & Grytnes, 2010) and/or that the increase in the strength of environmental filtering corresponds to where freezing temperatures occur along the elevational gradient. Indeed, our results are consistent with those of macroecological studies (Qian et al., 2017; Segovia et al., 2020), which report greater phylogenetic relatedness of trees (i.e. low phylogenetic diversity) in colder and drier biomes, a pattern driven by the evolution of traits to tolerate freezing temperatures and prolonged periods of drought. Differences in competitive ability also may underlie the observed shifts in functional diversity, where niche differences may lead to greater functional diversity at lower elevations and smaller differences in competitive ability may result in lower functional diversity at higher elevations (Mayfield & Levine, 2010). Low functional redundancy at higher elevations of 3000 – 3500 m suggests that these tree communities are functionally similar - possibly due to differences in competitive ability (Mayfield & Levine, 2010) - because they are dominated by a few species of conifers adapted to harsh environmental conditions. Consequently, these tree communities may be less resilient to species loss or future climate change (Fadrique et al., 2018).

Our results revealed that the impacts of forest-use intensity on functional diversity and redundancy in degraded and secondary forests were not consistent across elevations. At certain elevations, forest-use intensity affected functional diversity and functional redundancy, while for functional diversity at 1000 m, we detected significant differences between old-growth and secondary forests, with the highest functional diversity in secondary forests. While unexpected, this result is in line with previous studies that have shown variable responses of functional diversity to land-use intensity (e.g. Flynn et al., 2009). For functional redundancy, we found significant differences between old-

growth, degraded, and secondary forests at 0 m, and between degraded and secondary forests at 1500 m, which is consistent with previous studies in tropical and subtropical forests (Laliberté et al., 2010) and suggests that an increase in forest-use intensity may result in a decrease of functional redundancy. However, in other cases, forest-use intensity has also been shown to increase functional redundancy (Laliberté et al., 2010). In our study, forest-use intensity did not significantly affect functional redundancy at five out of eight elevations, suggesting that ecosystem processes of tropical forests can be resilient to forest uses of varying intensities (Norden et al., 2009).

Effects of forest structure on biodiversity facets

We found that all studied facets of biodiversity were higher in more structurally heterogeneous forests. Indeed, our results coincide with recent studies showing that structural heterogeneity promotes functional diversity (Ehbrecht et al., 2021; Hakkenberg et al., 2016). However, the positive effects of structural heterogeneity were only observed for biodiversity facets with Hill number 0, suggesting that forest structure had differential effects on functionally common and rare species. This indicates that disturbances or forest uses that simplify forest structure negatively impact the niche space of functionally unique species (Heidrich et al., 2020). Therefore, our results suggest that structurally heterogeneous forests should be conserved, while structurally simple forests should be actively managed to promote greater structural complexity. One promising silvicultural technique to achieve this is variable-density thinning that has been used successfully in temperate secondary forests to improve the functional composition of regeneration (Donoso et al., 2020). While such forest management techniques are not commonly used in tropical forests, the underlying ecological principles, e.g. niche partitioning, should also apply (Ashton et al., 2001).

Relationships between functional diversity, redundancy, and species diversity

A key result of our study is that functional diversity and redundancy reveal complementary insights into the role played by biodiversity in tropical forest ecosystems. First, the saturating relationship of functional diversity with species diversity across all Hill numbers suggests that recovery of ecosystem

functioning likely occurs quickly, as the initial, rapid accumulation of functionally unique species likely leads to a parallel increase in ecosystem functioning (Bagousse-Pinguet et al., 2021), via mechanisms such as niche complementarity (Barry et al., 2019). Second, the strong, positive relationship of functional redundancy and species diversity indicates that high-diversity forests also tend to have more functionally similar species than low-diversity forests and are therefore more resilient. This highlights the greater vulnerability of low-diversity, high-elevation forests in our study to biodiversity loss, where losing just a single species would likely have disproportionate impacts on ecosystem functioning. Because environmental filters impose strong constraints on the number of species that can persist at high elevations, managing for greater structural heterogeneity in these forests may not lead to increased resilience via greater species or functional diversity. Consequently, a more viable management strategy in these high-elevation forests could be enrichment plantings (Ashton et al., 2001; Griscom & Ashton, 2011) using native species known to tolerate current (and future) environmental conditions (Sacco et al., *in press*).

Conclusions

Our results suggest that forests with high species diversity are also more resilient. We found that high-elevation forests were functionally less redundant and consequently less resilient than forests at lower elevations. The high-elevation forests in our study thus appear to be most vulnerable to anthropogenic or climatic disturbances, because of small species pools and low stand heterogeneity. We suggest that efforts to enhance structural heterogeneity should lead to more functionally diverse and redundant forests. This can be achieved by conserving structural heterogeneity of existing old-growth forests, and by silvicultural interventions that increase structural heterogeneity. Doing so should have positive effects for the conservation of species diversity (particularly of rare species) as well as for the provisioning of ecosystem functioning. In conclusion, our results suggest that forest biodiversity will be increased if management promotes forests with high structural heterogeneity and the reduction of forest-use intensity, especially at high elevations where forests are particularly vulnerable to biodiversity loss.

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Authors' contributions

M.L.M-G, H.K., D.C. and T.K. conceived the study; M.L.M-G collected the data; M.L.M-G, D.C., and N.G-R. analyzed the data and wrote the paper with contributions from all authors. All authors contributed critically and gave final approval for publication.

Conflict of Interest

The authors have declared no conflicts of interest.

Data availability statement

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.ht76hdrg1> (Monge-González et al., 2021). The complete database for tree diversity, composition, functional traits and structure for the BIOVERA Project is publicly available (Monge-González et al., 2021a).

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Table 1. Results of analyses of variance (ANOVA) for models evaluating the interactive effects of elevation and forest-use intensity and forest structure (stem density, Gini coefficient and basal area) on functional diversity, functional redundancy using effective number of species, i.e., Hill numbers q = 0 (richness), q = 1 (Shannon diversity), and q = 2 (Simpson diversity). Bold values are statistically significant at <0.05. Degrees of freedom: elevation 7,84; forest-use intensity 2,84; stem density 1,84; forest structure 1,84; basal area 1,84; elevation x forest-use intensity 14,84.

| | | Functional diversity | | | Redundancy | | | Species diversity | | |
|-------------------------------|---------|----------------------|------------------|------------------|------------------|------------------|------------------|-------------------|------------------|------------------|
| | | q=0 | q=1 | q=2 | q=0 | q=1 | q=2 | q=0 | q=1 | q=2 |
| Elevation | F-value | 15.22 | 11.25 | 9.6 | 15.77 | 11.70 | 8.39 | 21.52 | 18.03 | 14.09 |
| | p-value | 1.05 e-12 | 5.61 e-10 | 1.02 e-08 | 4.77 e-13 | 3.10 e-10 | 9.46 e-08 | 2.35 e-16 | 2.04 e-14 | 5.82 e-12 |
| Forest-use intensity | F-value | 1.47 | 2.16 | 2.68 | 3.98 | 4.4 | 3.73 | 4.21 | 5.60 | 5.53 |
| | p-value | 0.23 | 0.12 | 0.07 | 0.02 | 0.01 | 0.02 | 0.01 | 0.005 | 0.005 |
| Stem density | F-value | 2.48 | 0.06 | 0 | 4.86 | 0.006 | 0.07 | 7.48 | 0.32 | 0.0006 |
| | p-value | 0.11 | 0.80 | 0.99 | 0.03 | 0.93 | 0.79 | 0.007 | 0.56 | 0.98 |
| Gini coefficient | F-value | 4.26 | 0.01 | 1.29 | 1.5 | 1.03 | 1.15 | 5.23 | 1.73 | 1.20 |
| | p-value | 0.04 | 0.91 | 0.25 | 0.21 | 0.31 | 0.28 | 0.02 | 0.19 | 0.27 |
| Basal area | F-value | 0.0006 | 0.01 | 0 | 1.4 | 1.69 | 0.76 | 0.03 | 0.79 | 0.66 |
| | p-value | 0.97 | 0.91 | 0.99 | 0.23 | 0.19 | 0.38 | 0.84 | 0.37 | 0.41 |
| Elevation x Forest-use | F-value | 1.99 | 2.60 | 2.51 | 4.21 | 4.74 | 4.11 | 3.54 | 4.19 | 3.87 |
| | p-value | 0.02 | 0.003 | 0.004 | 1.46 e-05 | 2.57 e-06 | 2.02 | 0.0001 | 1.58 e-05 | 4.55 e-05 |

intensity

| | | | | | | | | | |
|----------------|------|------|------|------|------|------|------|------|------|
| R ² | 0.79 | 0.75 | 0.72 | 0.84 | 0.78 | 0.72 | 0.87 | 0.84 | 0.80 |
|----------------|------|------|------|------|------|------|------|------|------|

Accepted Article Figures

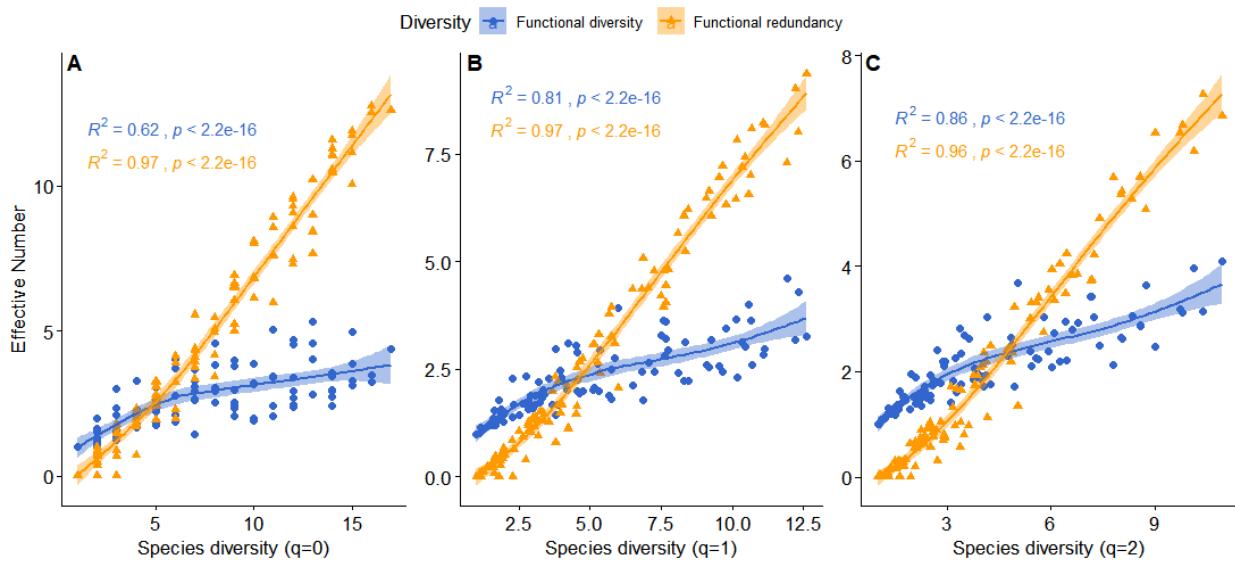


Figure 1. Relationships between functional diversity and redundancy and species diversity across tropical forests at different elevations in Veracruz, Mexico for Hill numbers **A)** 0, **B)** 1, and **C)** 2. Effective number of species (x-axes) or functional groups (y-axes) were calculated irrespective of species or functional groups abundance (Hill number 0, Richness) or weighted by abundance of common (Hill number 1, i.e. Shannon diversity) or abundant species or functional groups (Hill number 2, i.e. Simpson diversity). For redundancy, effective numbers elucidating if the ecological function of losing species can be replaced by another species in the community, irrespective of their abundance (Hill number 0) or when common or abundant species (Hill numbers 1 and 2, respectively) are considered. Relationships between functional diversity (in blue) and redundancy (in yellow) and species diversity were quantified using Spearman's correlations ($n = 111$ plots).

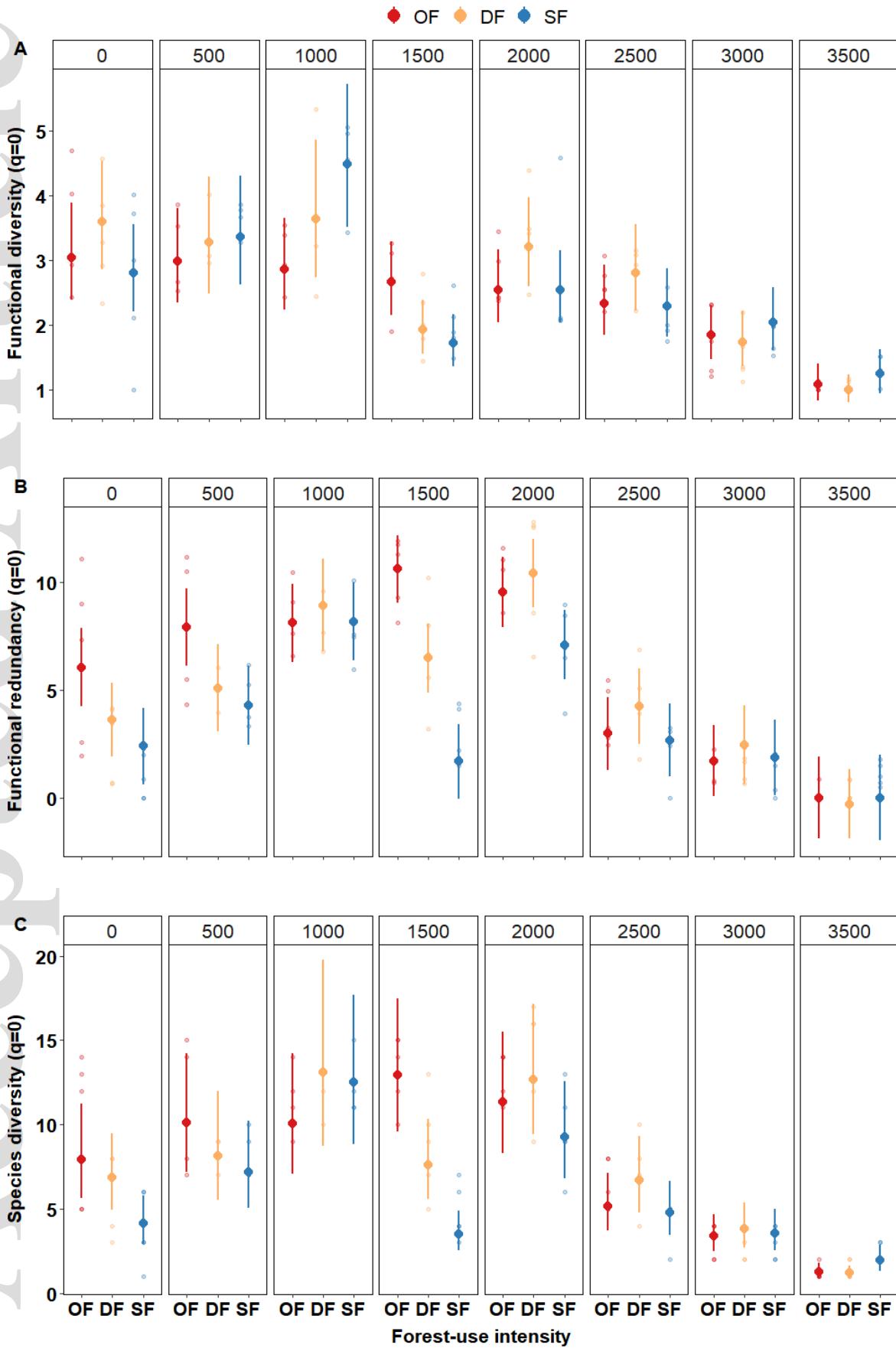


Figure 2. Different facets of biodiversity (Hill number $q = 0$) along the elevation gradient and at different levels of forest-use intensity ($n = 111$ plots). The interaction between elevation and forest-use intensity significantly explained **A)** functional diversity ($F_{14,84} = 1.99$, p-value = 0.02), **B)** redundancy ($F_{14,84} = 4.21$, p-value = 1.46×10^{-5}), and **C)** species diversity ($F_{14,84} = 3.54$, p-value = 0.0001). Bold points are predicted means, lines are 95% confidence intervals. Light points are plot-level values. Forest-use intensity levels are old-growth forest (OF), degraded forest (DF), and secondary forest (SF).

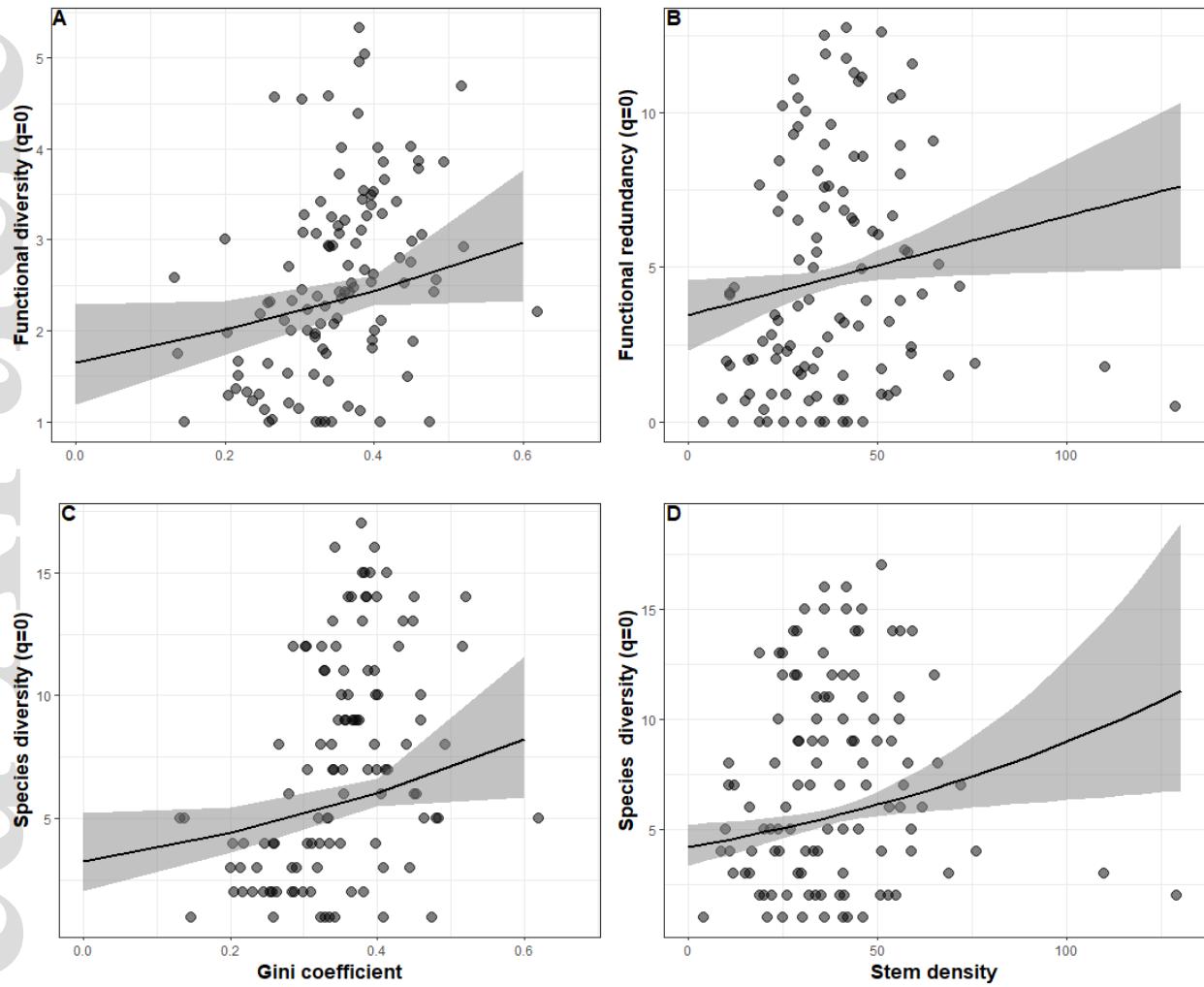


Figure 3. Different facets of biodiversity (Hill number $q = 0$) were explained significantly by forest structure, with: **A)** functional diversity explained by Gini coefficient of DBH ($F_{1,84} = 4.26$, p-value = 0.04), **B)** functional redundancy explained by stem density ($F_{1,84} = 4.86$, p-value = 0.03), **C)** species diversity explained by Gini coefficient ($F_{1,84} = 5.23$, p-value = 0.02), and **D)** by stem density ($F_{1,84} = 7.48$, p-value = 0.007). Solid lines are model predictions and grey areas indicate 95% confidence intervals.