








Response of tree diversity and community composition to forest use intensity along a tropical elevational gradient

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Abstract

Question: Land-use change and intensification are currently the most pervasive threats to tropical biodiversity. Yet, their effects on biodiversity change with elevation are unknown. Here, we examine how tree diversity and community composition vary with elevation and how the effects of forest use intensity on tree diversity and community composition change within elevations.

Location: Eastern slopes of the Cofre de Perote mountain, state of Veracruz, Mexico.

Methods: We assessed tree diversity and composition using a sampling design in which elevation was crossed with three levels of forest use intensity: old-growth, degraded, and secondary forests. We established 120 20 m × 20 m forest plots, located at eight sites between 0 m and 3,545 m. At each site, five replicate plots were inventoried for each level of forest use intensity.

Results: Our analyses revealed an interactive effect between elevation and forest use intensity affecting tree diversity and community composition along the elevational gradient. Contrasting effects of forest use intensity within elevation resulted in tree diversity following a low-plateau pattern for old-growth and a bimodal pattern for degraded and secondary forests. Along the entire elevational gradient, there were 217 tree species distributed within 154 genera and 80 families. Species accumulation curves revealed that forests at 0 m and 1,500 m elevation showed differences in species richness among forest use intensities. In contrast, species richness did not differ between old-growth forest and the other forest use intensities in five of the eight studied elevations. In terms of community composition, secondary forests differed from old-growth and degraded forests.

Conclusion: Our results suggest that the interactive effects of elevation and forest use intensity change tree diversity patterns and community composition along a tropical elevational gradient. Degraded forests were similar to old-growth forests in terms of species diversity and composition, suggesting that they may act as a safeguard of tree diversity in human-dominated tropical landscapes.

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KEYWORDS

degraded forest, elevational gradient, land use, Mexico, old-growth forest, secondary forest, tropical montane forest

1 | INTRODUCTION

Tropical mountains are characterized by steep gradients in climate and other environmental conditions that lead to rapid changes in diversity and species composition with elevation. Globally, tropical mountains are centers of plant diversity and endemism (Barthlott, Mutke, Rafiqpoor, Kier, & Kreft, 2005; Kier et al., 2009) resulting from the high environmental heterogeneity that affects both ecological and evolutionary processes (Antonelli et al., 2018; Stein, Gerstner, & Kreft, 2014). Tropical elevational gradients are considered natural laboratories where drivers of diversity patterns and ecosystem functions can be studied over short geographical distances (Körner et al., 2017; Sanders & Rahbek, 2012). However, tropical mountain ecosystems are also highly vulnerable to land use (Kidane, Stahlmann, & Beierkuhnlein, 2012; Malhi et al., 2010) and climate change (Cuesta et al., 2017), yet our understanding of how anthropogenic change may affect plant diversity and community composition along elevational gradients remains limited (Peters et al., 2019).

In tropical mountain ecosystems, tree diversity often peaks at mid-elevations (Clark, Hurtado, & Saatchi, 2015; Huerta Martínez, Briones Tirado, Neri Luna, Muñoz Urías, & Rosas Espinoza, 2014; Rutten, Ensslin, Hemp, & Fischer, 2015; Toledo-Garibaldi & Williams-Linera, 2014) or decreases monotonically with increasing elevation from the lowlands up (Aiba & Kitayama, 1999; Homeier, Breckle, Günter, Rollenbeck, & Leuschner, 2010; Slik et al., 2009). Explanations for the elevational gradients in tree diversity have focused principally on temperature and precipitation, soil nutrient concentrations, the mixing of biotas, spatial constraints associated with area and mid-domain effects, and – to a lesser extent – anthropogenic disturbances (Homeier et al., 2010; Peters et al., 2019; Rana, Gross, & Price, 2019; Slik et al., 2019; Toledo-Garibaldi & Williams-Linera, 2005; Zhang, Xu, & Li, 2013). The effect of land use type and intensity on species richness and composition might change along elevational gradients (McCain & Grytnes, 2010), as it might be amplified or weakened by climate changing with elevation (Peters et al., 2019). For example, if the impact of land use on diversity is higher at lower elevations than at higher elevations, species richness patterns could shift from monotonic to hump-shaped. Conversely, if the impact of land use on diversity is stronger at mid-elevations than at lower ones, species richness patterns could change from hump-shaped to monotonic.

Forest use intensity, from here on in defined as the conversion of (near-) natural, complex structured forest ecosystems to simplified, managed ecosystems with more frequent resource use or extraction (Nepstad, Uhl, Pereira, da Silva, & da Silva, 1996; Tschardt, Klein, Krüss, Steffan-Dewenter, & Thies, 2013; Vitousek, Mooney, Lubchenco, & Melillo, 1997), may also influence the composition of

forest communities by altering environmental conditions. In tropical forest ecosystems, highly intensive forest uses, such as cattle grazing and agroforestry, increase light availability and air temperature, reduce air humidity and soil moisture and have negative effects on propagule dispersion (Holl, 1999; Lebrija-Trejos, Pérez-García, Meave, Poorter, & Bongers, 2011). High forest use intensity may shift tree species composition to forests dominated by species better adapted to tolerate such conditions, e.g. fast-growing and light-demanding pioneer species, whereas more shade-tolerant late-successional species are often unable to persist (Craven, Hall, Berlyn, Ashton, & Breugel, 2015; Lohbeck et al., 2013). As a result of high-intensity forest use, light conditions increase and favor the establishment of early successional tree species. Therefore, floristic composition – and to a lesser extent species richness – of young secondary and degraded forests usually differs markedly from that of old-growth tropical forests (Gossner et al., 2013; Rozendaal et al., 2019). Yet, how such changes in species composition are mediated by climatic changes along elevational gradients is largely unknown (but see Peters et al., 2019).

Human impact on tropical mountain forests, such as logging and deforestation for agriculture, has transformed large parts of these ecosystems into human-dominated forested landscapes (Laurance, Sayer, & Cassman, 2014). Globally, the direction and magnitude of changes in species richness depend strongly on the kind, intensity, severity, incidence, and timing of disturbances (Barlow et al., 2018; Foley et al., 2005; Gibson et al., 2011; Newbold et al., 2015). Yet, we know little about the impacts of forest use intensity on tree diversity and composition along environmental gradients, particularly elevational gradients in tropical forests. While it is likely that these impacts will shift because tree communities differ in their resilience to similar forest uses (Crouzeilles et al., 2016), there is no a priori expectation whether the impacts will be stronger, weaker, or similar with changes in elevation.

Here, we examined how the interaction of elevation and forest use intensity affects tree diversity and community composition along an elevation gradient from sea level to treeline within a global biodiversity hotspot in central Veracruz, Mexico. Specifically, we asked: (a) how do tree diversity and community composition vary with elevation; and (b) how do the effects of forest use intensity on tree diversity and community composition change within elevational sites? We hypothesized that tree diversity monotonically decreases with increasing elevation (Aiba & Kitayama, 1999; Homeier et al., 2010; Slik et al., 2019; Toledo-Garibaldi & Williams-Linera, 2005), that high forest use intensity at lower elevations may shift species richness from monotonic to a hump-shaped pattern (McCain & Grytnes, 2010) and expected a consistently negative effect of forest use intensity on tree diversity and associated shifts in tree species composition (Gibson et al., 2011; Newbold et al., 2015).

2 | METHODS

2.1 | Study area

Our study was conducted along an elevational gradient, from sea level close to the Gulf of Mexico (19.5894 N, -96.375167 W) to close to the treeline at 3,545 m elevation (19.5182 N, -97.154525 W) along the eastern slopes of Cofre de Perote, an extinct volcano of 4,282 m in Veracruz, Mexico (Carvajal-Hernández & Krömer, 2015; Gómez-Díaz et al., 2017) (Figure 1). Climatic conditions along the elevational gradient vary from tropical-dry at lower elevations, to temperate-humid at mid-elevations and cold-dry at high elevations (Gómez-Díaz et al., 2017; Soto Esparza & Giddings Berger, 2011). Temperature decreases with elevation, with mean annual temperature ranging from 26°C near sea level to 9°C at the highest site. Mean annual precipitation varies from 1,222 mm at low elevations, 2,952 mm at mid-elevations and 708 mm at high elevations (Table 1).

The study area is located in the transition zone between two biogeographic regions, the Neotropical and Nearctic, in the Mesoamerican biodiversity hotspot (Morrone, 2006; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000). Biogeographically, the upper part of the elevational gradient falls into the convergence zone between the Trans-Mexican Volcanic Belt and the Sierra Madre Oriental (Rodríguez, Morales-Barrera, Layer, & González-Mercado, 2010). Along the elevation gradient, there are six main vegetation types including tropical semi-humid deciduous, tropical oak, humid montane, pine-oak, pine, and fir forests (Table 1; Leopold, 1950).

2.2 | Study design and data collection

The study was conducted at eight sites along the elevational gradient, separated by about 500 m in elevation (Figure 1). Hereafter, we refer

to every elevation as 0, 500, 1,000, 1,500, 2,000, 2,500, 3,000, and 3,500 m. At each site, we established 15 plots of 20 m × 20 m, including five plots each in old-growth, degraded, and secondary forests. In total, 120 non-permanent forest plots (4.8 ha) were inventoried. Forest use intensity was defined following Leuschner, Wiens, Harteveld, Hertel, and Tjitrosemito (2006), Carvajal-Hernández and Krömer (2015) and Gómez-Díaz et al. (2017): (a) old-growth forest (OF): a mature forest with tall, large-diameter trees and without any visible signs of recent human disturbance, classified as low forest use intensity; (b) degraded forest (DF): a forest subjected to selective logging and/ or cattle grazing, classified as intermediate forest use intensity; (c) secondary forest (SF): a young forest (15–20 years since abandonment) recovering after clearcutting, sometimes with cattle grazing, with small diameter trees, classified as high forest use intensity. In each plot, we measured and identified all trees with a diameter at breast height (DHB) ≥ 5 cm (Homeier et al., 2010; Toledo-Garibaldi & Williams-Linera, 2005). In total, 64.5% of the individuals could be identified to species level, 19.3% were identified to genus level, 8.2% to family level and 7.8% were unidentified species (see Appendix S1 for the tree species list; species names follow The Plant List version 1.1 [2013]). Tree species were identified by specialists (Dr. Francisco Lorea Hernández, M.Sc. Claudia Gallardo Hernández and Biol. Carlos M. Durán Espinosa, Instituto de Ecología, A. C.). Vouchers of specimens were deposited at the herbarium XAL of Instituto de Ecología, A.C. at Xalapa, Mexico. The sampling was conducted from November 2015 to August 2016.

2.3 | Analysis of tree diversity

We estimated species diversity as species richness (Hill number $q = 0$), Shannon diversity ($q = 1$), and Simpson diversity ($q = 2$) in terms of effective species numbers (Jost, 2006). These diversity

FIGURE 1 Location of the eight study sites along the elevational gradient of the eastern slopes of Cofre de Perote in Veracruz, Mexico. Black dots show the location of sites: (1) 0 m; (2) 500 m; (3) 1,000 m; (4) 1,500 m; (5) 2,000 m; (6) 2,500 m; (7) 3,000 m; (8) 3,500 m [Colour figure can be viewed at wileyonlinelibrary.com]

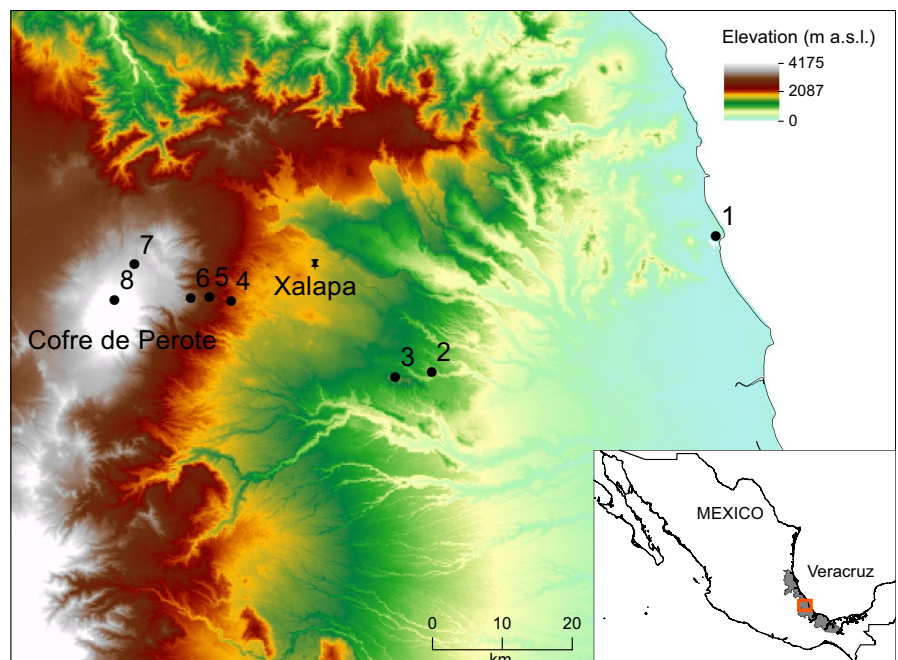


TABLE 1 Location and climatic conditions of the eight study sites in central Veracruz, Mexico

Site	Elevation (m)	N latitude	W longitude	MAT (°C)	MAP (mm/a)	Vegetation type
1	0–60	19.58	–96.37	26	1,222	Tropical semi-humid deciduous forest
2	569–695	19.54	–96.89	23	946	Tropical oak forest
3	913–1,023	19.42	–96.79	21	1,331	Tropical oak forest
4	1,501–1,650	19.52	–96.98	19	1,436	Humid montane forest
5	2,008–2,240	19.51	–97.03	14	2,952	Humid montane forest
6	2,487–2,575	19.52	–97.05	12	1,104	Pine-oak forest
7	3,014–3,139	19.56	–97.13	9	708	Pine forest
8	3,305–3,545	19.51	–97.15	9	708	Fir forest

Note: Vegetation types according to Leopold (1950); MAT, mean annual temperature (°C); MAP, mean annual precipitation (mm/a). Climate data were obtained from National Meteorological Service of México (SMN, 2019) for 1951–2010.

indices give increasing weight to species abundances; while species richness gives equal weight to common and rare species, Shannon and Simpson diversities emphasize the contributions of common and abundant species, respectively. For each diversity index, we estimated species accumulation curves using sample-based rarefaction and extrapolation (Chao et al., 2014), pooling data by forest use intensity for each elevation. We used rarefaction and extrapolation because the number of individuals may vary systematically with forest use intensity, which may bias estimates of species diversity in plots with more individuals. As we observed similar patterns for Shannon and Simpson diversities, we only present and discuss results for species richness. At the plot level, we estimated species diversity using a fixed sample coverage of 95% with the 'iNEXT' package (Hsieh, Ma, & Chao, 2016) to permit unbiased comparisons of species diversity across forest use intensities and elevations. To meet model assumptions of normality, we natural-log-transformed all diversity indices.

At the plot level, we examined the effect of forest use intensity at each elevation on species richness and Shannon and Simpson diversities by a nested analysis of variance (ANOVA) using the R function *aov*, where forest use intensity and elevation were treated as categorical variables. We performed post-hoc comparisons using a Tukey's Honest Significant Differences test with the packages 'car' (Fox & Weisberg, 2011) and 'multcomp' (Hothorn, Bretz, & Westfall, 2008).

We examined changes in tree community composition among elevational sites and levels of forest use intensity using non-metric multidimensional scaling (NMDS) with both incidence-based Jaccard dissimilarity and abundance-based Bray–Curtis dissimilarity (adjustment *noshare* = 0.1; 999 permutations) using the packages *ecodist* (Goslee & Urban, 2007) and *vegan* (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). We then tested for differences in tree community composition across elevations and levels of forest use intensity with a nested permutational multivariate analysis of variance (PERMANOVA, 999 permutations) using the *adonis* function in the *vegan* package (R Core Team, R Foundation for Statistical Computing, Vienna, Austria), followed by pairwise comparisons using the *pairwise.adonis* function in the *pairwiseAdonis* package. The *p*-values for the pairwise comparisons were Bonferroni-corrected to

test differences in species composition among levels of forest use intensity within elevation. For data manipulation and visualization, we used the R packages 'dplyr' (R Core Team, R Foundation for Statistical Computing, Vienna, Austria) and 'ggplot2' (Springer-Verlag, New York, NY, USA), respectively. We performed all analyses in R version 3.5.1 (R Core Team, 2018).

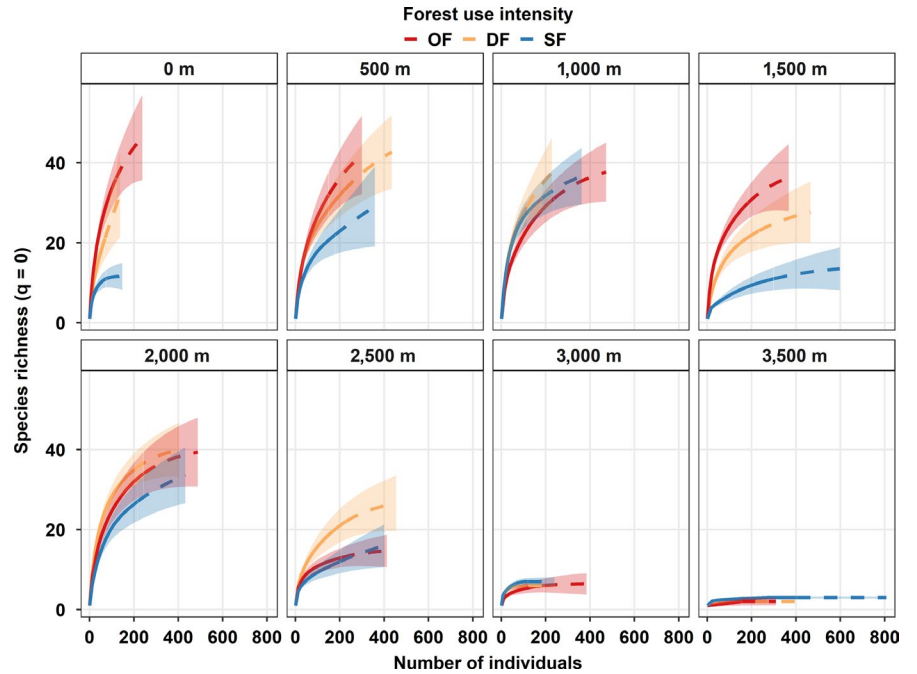
3 | RESULTS

3.1 | Changes in tree diversity along the elevation gradient

We recorded a total of 4,555 individual trees belonging to 217 species distributed among 80 families and 154 genera (Appendix S1). The most diverse families were Fagaceae (15 species), Leguminosae (13), Moraceae (10), and Pinaceae (8). At lower elevations (below 1,000 m), tropical genera such as *Ficus*, *Acacia*, and *Bursera* were the most abundant, while at mid-elevations *Quercus*, *Carpinus*, and *Liquidambar* and at 2,500 m (transitional pine–oak forest) *Pinus*, *Quercus*, and *Juniperus* were the most common. At higher elevations (3,000–3,500 m), the most abundant genera were *Abies*, *Pinus*, and *Alnus*. Across all elevations, 18% of all species exclusively occurred in old-growth forest followed by 16% in secondary forest, and 9% in degraded forest.

At most elevations (500, 1,000, 2,000, 3,000 and 3,500 m) species accumulation curves overlapped across forest use intensities, revealing that species pools of degraded and secondary forests were of similar size (indicated by overlapping 95% confidence intervals) as those of old-growth forests (Figure 2). In contrast, at 0 and 1,500 m species accumulation curves showed significant differences in species richness between forest use intensities (95% confidence intervals did not overlap). Species accumulation curves at 2,500 m showed that the tree species richness in degraded forests was higher than the species richness of old-growth forests (Figure 2). For most levels of forest use intensity, species accumulation curves did not reach an asymptote at elevations between 0 and 2,500 m (except for secondary forests at 0 m). At 3,000 and 3,500 m, species accumulation curves for all levels

FIGURE 2 Rarefaction (solid lines) and extrapolated (dashed lines) curves for species richness (Hill number $q = 0$, pooling data by forest use intensity within each elevation). Shaded areas are the 95% confidence intervals. Forest use intensity levels are: old-growth forest (OF, red), degraded forest (DF, yellow) and secondary forest (SF, blue) [Colour figure can be viewed at wileyonlinelibrary.com]



of forest use intensity reached an asymptote, indicating that these forests have been fully sampled (Figure 2).

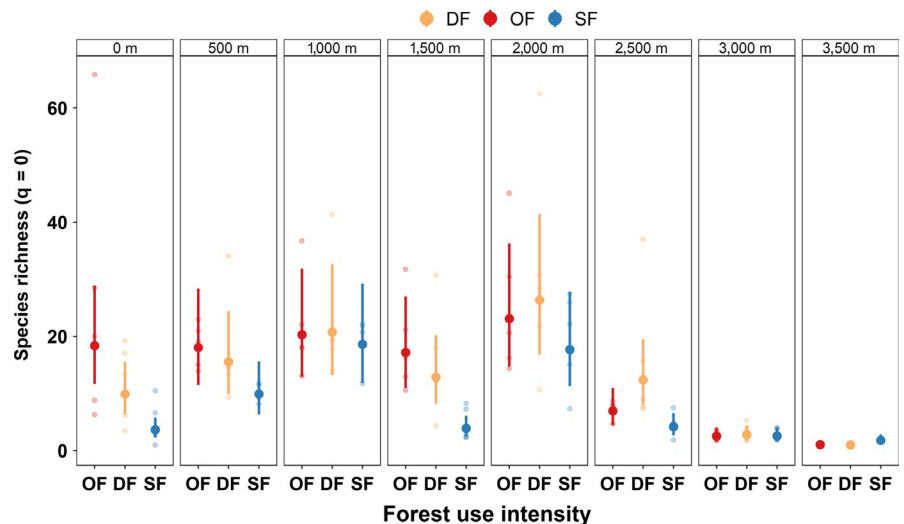
3.2 | Effects of forest use intensity on local tree species diversity along the elevation gradient

Elevation significantly affected plot-level tree species richness (Hill number $q = 0$; $F_{7,96} = 57.02$, p -value < 0.001), Shannon diversity (Hill number $q = 1$; $F_{7,96} = 49.44$, p -value < 0.001) and Simpson diversity (Hill number $q = 2$; $F_{7,96} = 37.74$, p -value < 0.001; Appendix S2). Within elevations, tree diversity varied significantly among forest use intensity levels ($F_{16,96} = 4.38$ for species richness, $F_{16,97} = 5.47$ for Shannon diversity and, $F_{16,96} = 4.91$ for Simpson diversity, p -value < 0.001; Appendix S2).

Pairwise comparisons among forest use intensity levels within elevations showed significant differences in tree species richness between old-growth and secondary forests at 0, 500, 1,500 and 3,500 m (p -value < 0.05; Appendix S3; Figure 3). While these differences were associated with higher species richness in old-growth forests than in secondary forests at 0, 500 and 1,500 m, the inverse pattern was observed at 3,500 m, i.e., higher species richness in secondary forests than in old-growth forests. Similarly, we found significant differences in tree species richness between degraded and secondary forests at 1,500, 2,500 and 3,500 m (p -value < 0.05; Appendix S3), with higher tree species richness in degraded than in secondary forests at 1,500 and 2,500 m but the inverse trend at 3,500 m.

In old-growth forests, tree species richness along the elevational gradient was best described as a low-plateau pattern, where species

FIGURE 3 Tree species richness (Hill number $q = 0$) along the elevation gradient and different levels of forest use intensity ($n = 120$ plots). Tree species richness was significantly affected by elevation ($F_{7,96} = 57.02$, p -value < 0.001) and forest use intensity within elevation ($F_{16,96} = 4.38$, p -value < 0.001; Appendix S2). Bold points are predicted means from a nested ANOVA (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) [Colour figure can be viewed at wileyonlinelibrary.com]



richness was highest from 0 to 2000 m, after which it decreased monotonically (Figure 3). Tree species richness in degraded and secondary forests showed a bimodal pattern with peaks at 1,000 and 2,000 m, declining towards both ends of the elevational gradient (Figure 3). Similar patterns were observed for Shannon and Simpson diversities (Appendices S8, S9).

3.3 | Tree community composition among gradients of forest use intensity and elevation

We found that tree community composition varied significantly along the elevational gradient (PERMANOVA $F_{7,96} = 8.69$, $R^2 = 0.30$, p -value < 0.001 and $F_{7,96} = 14.94$, $R^2 = 0.40$, p -value < 0.001 based on Jaccard and Bray–Curtis dissimilarity, respectively; Appendices S6, S7) and among forest use intensity levels within elevation (PERMANOVA $F_{16,96} = 2.88$, $R^2 = 0.23$, p -value < 0.001 and $F_{16,96} = 3.82$, $R^2 = 0.23$, p -value < 0.001 based on Jaccard and Bray–Curtis dissimilarity, respectively; Appendices S4, S5). Within elevations, floristic composition differed significantly between old-growth forest and secondary forest (adjusted p -value < 0.05), except at 2,500 m (Figure 4; Appendices S6, S7, S10). In contrast, within elevations, floristic composition only varied significantly between old-growth and degraded forests at 500, 1,000 and 1,500 m based on Jaccard dissimilarity and at 1,000 and 1,500 m based on Bray–Curtis dissimilarity (p -value adjusted < 0.05 ; Appendices S9, S10). At these elevations, floristic composition differed significantly among old-growth, degraded and secondary forests (pairwise comparisons within elevation, p -value adjusted < 0.05 ; Figure 4; Appendices S6, S7, S10). Tree community composition varied between degraded and secondary forests in most elevations except at 2,000 and

3,000 m based on Jaccard dissimilarity and at 500, 2,000, and 3,000 m based on Bray–Curtis dissimilarity (Appendices S6, S7, S10).

4 | DISCUSSION

Our results revealed that the interaction between elevation and forest use intensity affected tree diversity, i.e. species richness, Shannon and Simpson diversity as well as community composition. Importantly, we found that the effects of forest use intensity on tree diversity were not consistent along the elevational gradient, with tree diversity decreasing significantly in secondary compared with old-growth forests at only three elevations (0, 500 and 1,500 m). Together, our results suggest that the direction and magnitude of the effects of anthropogenic forest disturbance on tree diversity in tropical forests are context-dependent and will be difficult to generalize more broadly.

4.1 | Forest use intensity affects tree diversity along the elevational gradient

Forest use intensity affected tree diversity, and we found significant interactive effects of forest use intensity and elevation on diversity and species composition. While our analyses revealed that an increase in forest use intensity may result in a decrease of tree diversity, this pattern was not consistent along the elevational gradient. Anthropogenic forest use is generally thought to reduce species richness in tropical forest landscapes (Gibson et al., 2011; Kessler et al., 2009; Ramírez-Marcial, González-Espinosa, & Williams-Linera, 2019; Williams-Linera & Lorea, 2009). Yet the effects of land use

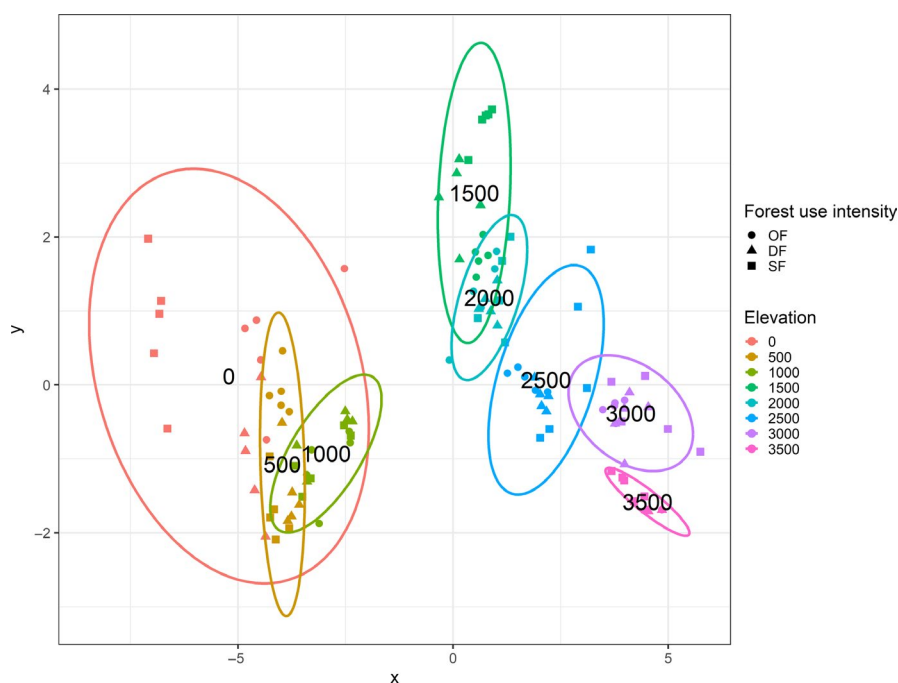


FIGURE 4 Tree community composition along eight elevational sites and three different forest use intensity levels. Non-metric multidimensional scaling (NMDS) based on Jaccard dissimilarity ($n = 5$ plots per forest use intensity within elevation), ellipses show the range of each elevation site. Forest use intensity levels are old-growth forest (OF, circles), degraded forest (DF, triangles) and secondary forest (SF, squares) [Colour figure can be viewed at wileyonlinelibrary.com]

change are context-dependent and depend on the timing, frequency, type and intensity of disturbances (Carreño-Rocabado et al., 2012; Newbold et al., 2015; Ramírez-Marcial et al., 2019), factors which likely varied along the elevational gradient in this study.

Old-growth and degraded forests exhibited similar plot-level species diversity at all elevations, a pattern that is consistent with previous studies (Rutten et al., 2015; Zhang et al., 2013) and that suggests that high local-scale diversity can be maintained under moderate levels of disturbance. Furthermore, these results suggest that degraded forests may act as reservoirs of native tree diversity and, thus, play an important role in the conservation of diverse tropical forests (Chazdon et al., 2009; Rozendaal et al., 2015). A potential explanation of the observed pattern is that low or medium forest use intensities or the creation of gaps in the forest canopy may create new habitats that favor the establishment of fast-growing and light-demanding tree species (Ramírez-Marcial et al., 2001; Zhang et al., 2013) or may facilitate the growth of advanced regeneration of shade-tolerant species into larger size classes (Brokaw, 1985; Denslow, 1987). However, forests subjected to frequent disturbances may be vulnerable to biological invasions in the future (Alpert, Bone, & Holzapfel, 2000), although we did not detect the presence of any non-native woody species in our inventory. On the other hand, we found that secondary forests had lower tree diversity compared to old-growth forests at half of the elevational sites. This suggests that high forest use intensity reduces diversity and that tree communities, particularly old-growth forests, need more time to recover in species composition (Crouzeilles et al., 2016; Gossner et al., 2016; Peters et al., 2019; Rozendaal et al., 2015). Yet the effects of both low and high forest use intensity, and the subsequent trajectory of recovery, may depend on intrinsic biotic and abiotic conditions within each elevation, e.g. differences in dispersal limitation, distance from adjacent forest, and propagule sources (Holl, 1999; Martínez-Garza & González-Montagut 1999; van Breugel et al., 2013).

The interactive effects of elevation and forest use intensity resulted in contrasting tree diversity patterns along the elevational gradient. The low-plateau elevational gradient for tree diversity in old-growth forests gradually changed into a bimodal pattern for degraded and especially secondary forests. These results are broadly in line with a recent multi-taxon study from Mount Kilimanjaro in Tanzania that showed interactive effects of climate and land use change on diversity trends (Peters et al., 2019). Specifically, in our study, the low plateau pattern in old-growth forest was driven by similar values in species richness between sea level and 2,000 m, above which it decreased strongly towards the treeline. Such an elevational pattern in tree diversity has been described before, although it appears to be uncommon (Jankowski et al., 2013; Rana et al., 2010). The high species diversity between sea level and 2,000 m may be linked to climatic conditions; for instance, tree diversity usually increases with temperature and precipitation (Homeier et al., 2010; Toledo-Garibaldi & Williams-Linera, 2005). In this regard, it is interesting that the highest species richness observed in our study occurred in the warm

but comparatively dry lowlands (Portillo-Quintero & Sánchez-Azofeifa, 2010). However, this observation is in line with previous studies concerning trees along elevational gradients showing that temperature is the primary climatic predictor of tree diversity and stronger than precipitation (Sharma, Behera, Das, & Panda, 2019; Toledo-Garibaldi & Williams-Linera, 2005). We attribute the sharp decrease in tree diversity above 2,000 m mainly to low minimum temperatures and the frequent occurrence of frost (-3°C absolute minimum temperature in winter; Pereyra, Palma, & G., & Zitacuaro C. I., 1992; Toledo-Garibaldi & Williams-Linera, 2005; C.I. Carvajal-Hernández, unpublished data). These thermal conditions represent strong biophysical constraints that likely limit the occurrence of tropical tree species (Veintimilla et al., 2019; Zanne et al., 2014), which is consistent with patterns reported from the Himalayas by Bhattarai and Vetaas (2006) and Rana et al. (2010). Interestingly, this decrease in tree diversity above 2,000 m was also observed for degraded and secondary forests, suggesting a strong role of ecological factors associated with elevation.

4.2 | Floristic composition along the elevational gradient and forest use intensity

We found marked differences in tree composition related to forest use intensity at most elevations, especially between old-growth and secondary forests. This suggests that, at most elevations, high-intensity forest use strongly affected community composition, which supports results from previous studies in Neotropical forests (Norden, Chazdon, Chao, Jiang, & Vilchez-Alvarado, 2009; Dent et al., 2013; DeWalt, & Denslow, 3). This observed shift in forest composition may be explained by the fact that the time needed to recover species composition may be longer than that for species richness (Rozendaal et al., 2015), as strong environmental filtering in tropical secondary forests limits the diversity of adaptive trait combinations (Lebrija-Trejos et al., 2011). For instance, the abiotic conditions in secondary forests typically favor light-demanding, fast-growing species over shade-tolerant, slow-growing species, which are better adapted to abiotic conditions found in old-growth forests (Bazzaz & Pickett, 1980; Crouzeilles et al., 2016; Ewel, 1980; Finegan, 1984; Gómez-Pompa & Vásquez-Yanes, 1974; Guariguata & Ostertag, 2001; Swaine & Whitmore, 1988). Other factors may similarly contribute to the differentiation in species composition of old-growth and secondary forests, such as previous forest use type and proximity of seed sources (Guariguata & Ostertag, 2001; Muñoz-Castro, Williams-Linera, & Benayas, 2006; Rozendaal et al., 2015; Zhang et al., 2013). In contrast, the composition of tree communities did not vary significantly between old-growth and degraded forests within five or six of the eight studied elevations (based on incidence or abundance-based dissimilarities, respectively). This suggests that moderate forest use intensity in most degraded tropical forests did not appreciably alter abiotic conditions, as many common species (probably shade-tolerant, slow-growing

ones) that also occurred in old-growth forests were able to persist in degraded ones. Our finding is in line with that of a previous study on herbaceous species along the same elevational gradient, which also reported a similar floristic composition of old-growth and degraded forests (Gómez-Díaz et al., 2017). It is important to note that our study did not consider the possible impacts of forest use intensity on the tree seedling community, which may capture the impacts of disturbances more readily than the mature tree community (Alvarez-Aquino et al., 2004; Ramírez-Marcial, 2003). While forest disturbances of even moderate intensity may result in extinction debts in the long term (Moreno-Mateos et al., 2017), the similar floristic composition of old-growth and degraded forests at most elevations supports the idea that degraded forests may act as important reservoirs of biodiversity in human-modified tropical landscapes.

5 | CONCLUSIONS

We found that forest use intensity significantly altered tree species diversity and composition, and that this effect was modified by elevation. Our results provide evidence that, even in human-dominated tropical landscapes, degraded and secondary forests may safeguard considerable levels of tree diversity. Due to their greater similarity to old-growth forests, degraded forests may act as reservoirs for biodiversity conservation and restoration. In conclusion, the interactive effects between land use and elevation render predictions across elevations difficult and highlight the value of examining how forest use intensity may alter diversity patterns along elevational gradients in tropical forests.

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AUTHOR CONTRIBUTIONS

MLM-G, HK and TK conceived the study; MLM-G, AH-S and GC-C collected data; MLM-G, DC and NG-R analysed the data; MLM-G wrote the paper with contributions from HK, DC, NG-R, VG-J and TK; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Primary data are available in Appendix S1 of Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. List of tree species recorded at different levels of forest use intensity along an elevational gradient in central Veracruz, Mexico

Appendix S2. Additional results for the effects of elevation and forest use intensity on tree diversity and community composition, including analysis of variance (ANOVA) and Tukey contrasts for richness, Shannon and Simpson diversity and permutational multivariate analysis of variance (PERMANOVA) and pairwise comparisons for community composition using both Jaccard and Bray-Curtis dissimilarities

Appendix S3. Results of statistical analyses of multiple comparisons of means using Tukey Contrasts

Appendix S4. Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) evaluating the effects of elevation and forest-use intensity nested in elevation on tree community composition. Dissimilarity was estimated using incidence-based Jaccard dissimilarity and 999 permutations

Appendix S5. Results of the Permutational Multivariate Analysis of Variance (PERMANOVA) evaluating the effects of elevation and

forest-use intensity nested in elevation on tree community composition. Dissimilarity was estimated using abundance-based Bray Curtis dissimilarity and 999 permutations

Appendix S6. Results of statistical analysis of pairwise comparisons between tree community composition estimated using incidence-based Jaccard in every forest-use intensity and per each elevation

Appendix S7. Results of statistical analysis of pairwise comparisons between tree community composition estimated using abundance-based Bray Curtis in every forest-use intensity and per each elevation

Appendix S8. Tree species richness (Hill number = 1) along the elevation gradient and different levels of forest use intensity

Appendix S9. Tree species richness (Hill number = 2) along the elevation gradient and different levels of forest use intensity

Appendix S10. Tree community composition along eight elevational sites and three different forest-use intensity levels

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