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Transformation of natural habitat disrupts biogeographical patterns of orchid diversity

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ABSTRACT

Physical gradients are major natural drivers of global biodiversity. A key question is understanding how biogeographic patterns are impacted by transformation of natural habitats. We aim to elucidate the complex relationships between two core biogeographic drivers of biodiversity—elevation and precipitation—, local deforestation, and their additive and interactive effects on Andean orchid diversity in the Colombian Andes. We sampled understory orchids across 341 plots pairing natural and transformed habitats along a wide elevational (1163–3415 m) and precipitation range (879–3817 mm per year). We found 35,891 adult individuals in 341 species peaking at mid-elevations (~2500 m) and mid-to-high precipitations (>1600 mm/yr). Conversion of natural to transformed habitats caused substantial orchid diversity loss, with ten-fold fewer species at the plot level equating to a 6-fold loss in overall species richness, and 23-times fewer individuals. The additive and interactive effects better explained the main patterns: conversion reconfigured the natural mid-elevation trends in orchid diversity and positive trend in diversity with precipitation to a quasi-linear trend in transformed habitats. This reflects the inherent dependency of orchid species to a host tree as well as lower resilience to transformed habitats. Our findings highlight the importance of halting deforestation across environmental gradients, but in particular at elevations and precipitations where reshaping of biogeographic patterns maximises the losses of biodiversity.

1. Introduction

Physical gradients are strong global drivers of concentrations and rapid turn- over of species (Antonelli et al., 2018; Pérez-Escobar et al., 2022; Peters et al., 2016; Rahbek et al., 2019). For instance, abrupt changes in elevation or precipitation over short distances introduce barriers for species dispersal shaping biogeographic patterns of biodiversity. Evolutionary phylogenetic reconstruction of mountain floras shows taxon-dependant results, from highly restrictive barriers imposed by the events of mountainous uplift in the Himalayas (Kala Rana et al., 2022), to a semipermeable barrier for some orchids in the Northern Andes (Pérez-Escobar et al., 2017, 2022). Yet natural habitats are being converted to farmland at massive spatial scales that span biogeographic gradients (Ganuza et al., 2022; Peters et al., 2019). A key question, therefore, is how biogeographic patterns are impacted by conversion of mountainous natural habitats to human-dominated land-uses.

In unmodified systems, species richness of vascular plants is high in lowlands and decreases towards higher elevations in Africa and the Andes (Pérez-Escobar et al., 2022; Peters et al., 2016), whereas other studies show that Andean trees and epiphytic plant diversity peaks at mid-elevations (1400–1600 m for trees, Malizia et al., 2020; and ~1000 m and 1500 mfor epiphytes, Cardelus et al., 2006; Krömer et al., 2005). Higher elevations show a reduction in species richness of many taxa related to low temperatures and frequent frost events (>3000 m), but harbour other endemic taxa such as Andean frailejones (Espeletiinae, Asteraceae; Cortés et al., 2018; Lüttge, 1997). In turn, precipitation promotes water interception, ecosystem productivity, and reduces drought stress exerting a positive effect on species richness (Gotsch et al., 2016; Hu et al., 2022; Karger et al., 2021), with higher species diversity at higher precipitations (Antonelli et al., 2018), although at extremely high precipitation plant species richness might decrease (Peters et al., 2016; Santillán et al., 2018; Tolmos et al., 2022). This

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evidence shows that patterns and predictors of mountainous diversity appear to be context dependent due to the taxon-specific resource requirements and evolutionary adaptations to their natural environment (Cortés et al., 2018; Peters et al., 2016).

Between 1990 and 2019, 219 million hectares of tropical forests were deforested (Vancutsem et al., 2021). This conversion of natural habitats might affect natural biogeographical patterns. For instance, Andean birds are more severely impacted by habitat transformation at lower elevations (~1000 m), than above 2000 m (Mills et al., 2022), whilst in a multi-taxa study in African mountains the negative effects of habitat transformation are buffered at mid-elevations where the loss of fauna and flora is apparently offset by the effects of elevation (Peters et al., 2019). By contrast, epiphyte species richness has shown a mixed response between forest-use intensity and elevation (Guzmán-Jacob et al., 2020), whilst other studies have found high losses in species richness and total abundance regardless of the elevation and precipitation gradient independently (Barthlott et al., 2001; Einzmann and Zotz, 2017b; Köster et al., 2009; Parra-Sanchez and Banks-Leite, 2020, 2022). However, there is a big gap in understanding of the independent, additive, or interactive effects of habitat transformation and core biogeographic forces of mountainous biodiversity.

We tackle the key question of how habitat transformation influences diversity across the biogeographic gradients of elevation and precipitation, as two of the most influential drivers of biodiversity patterns (Antonelli et al., 2018; Pérez-Escobar et al., 2017; Rahbek et al., 2019a). We do so by focusing on the Colombian Andes, a global biodiversity hotspot that has undergone extensive human transformation (Rodríguez Eraso et al., 2013), and on the Orchidaceae, as the most hyperdiverse plant family in the Andean realm (Pérez-Escobar et al., 2022). Orchids show high species turnover across space and high sensitivity to local changes in habitat and geographical distance (Parra-Sanchez et al., 2023a; Wraith and Pickering, 2018). We aim to untangle the independent and interactive effects of biogeographic drivers (elevation and precipitation) in natural vs transformed habitats in shaping understory orchid communities. Specifically, we test four complementary hypotheses: whether the main source of variation in orchid diversity patterns is explained by biogeographic drivers alone (Hypothesis 1), local deforestation (H2), or their additive (H3) or interactive effects (H4). We expect that patterns in transformed habi- tats will mirror those in natural habitats across the elevational and precipitation gradients.

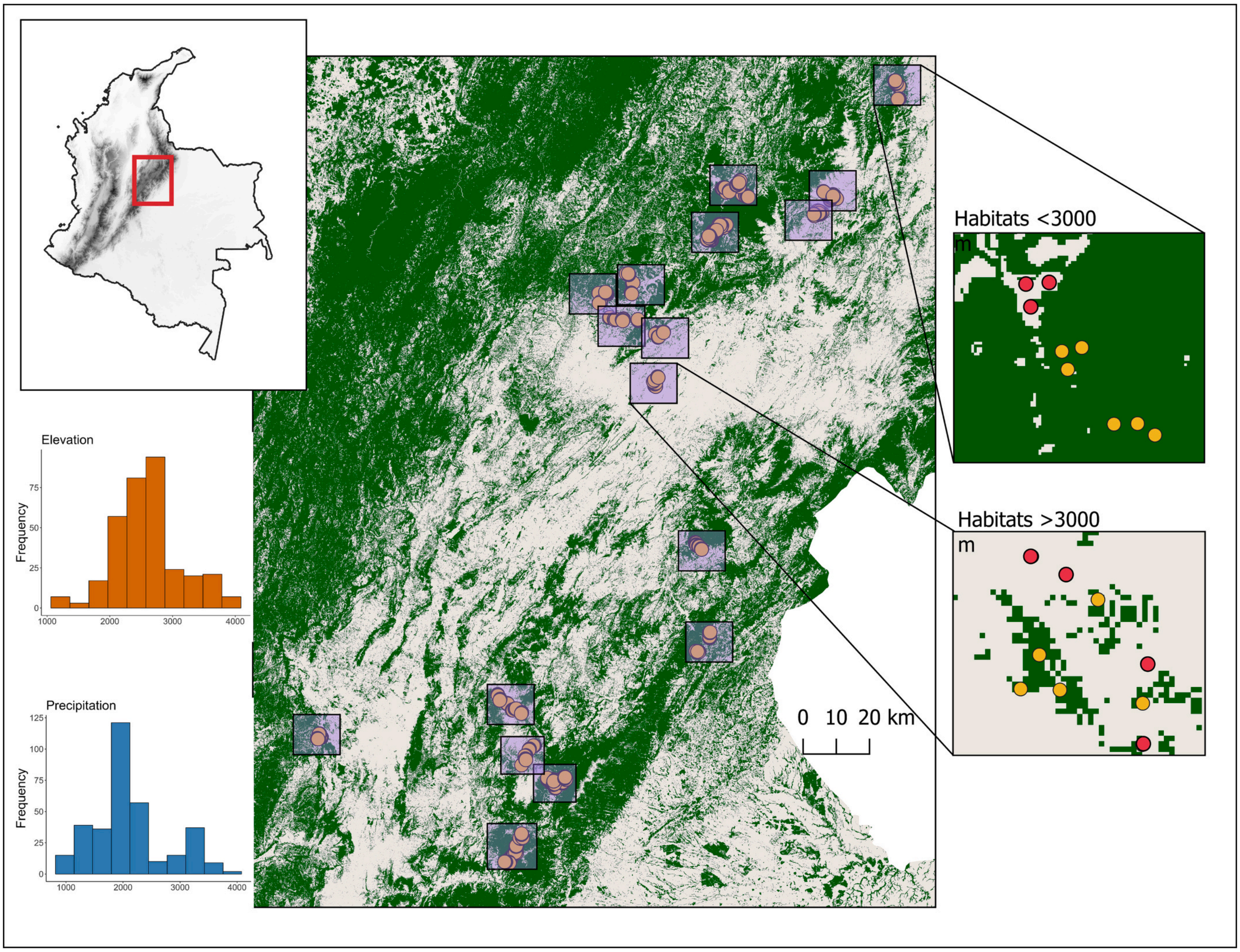

Fig. 1. Distribution of sampling plots and landscapes with their general precipitation and elevational characteristics in the study area, the eastern cordillera of the Colombian Andes. Inset panel displays study area within Colombia (red box), and elevation (digital elevation model from Tadono et al., 2014). The map shows the forest cover (green) and the absence of forest cover (grey; Vancutsem et al., 2021), landscapes (purple boxes), and sampling plots in natural (orange dots) and transformed habitats (red dots). Histograms display elevations (in metres above sea level; brick colour) and precipitation (in mm per year; blue colour) across sampling points. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Materials and methods

2.1. Study area

The study was located in the eastern cordillera of the Colombian Andes in the Departments of Cundinamarca, Boyacá, Meta, and Santander. Following Parra-Sanchez et al. (2023a), the random design covered the natural treeline. The treeline is the upper-limit boundary of the establishment of arboreal vegetation, between upper Andean montane forest and low-stature vegetation characterised by low canopy cover and encroached trees (Bader et al., 2007). Across the study area, we sampled 18 landscapes composed of natural and transformed habitats (Fig. 1). We surveyed natural habitats and pasture across a 2252 m elevational range (1163–3415 m) and a 2937 mm precipitation range (879–3817 mm per year). Natural habitats were composed of mountainous evergreen forests (bosque Andino and Altoandino; (Etter et al., 2021) with average cloud cover of 82 % (Wilson and Jetz, 2016), and paramo habitats above the treeline (~2900 m)). Paramo (>3000 m) included grasslands, shrublands, and high-elevation isolated forest patches (*Polylepis quadrijuga* Bitter). All sampled natural sites belonged to the network of protected areas in Colombia (Sistema nacional de areas protegidas -SINAP, Santuario de Fauna de Flora de Iguaque and Parque Natural Chingaza).

Natural habitat plots were paired with pasturelands as open habitats that have been completely transformed by human activities mainly for cattle production (n = 18 landscapes). Below the treeline (1163–2900 m), we paired forests with nearby pastures, and above the treeline, natural paramo habitats were paired with high elevational pasturelands (Fig. 1; >2900 m). The vegetation in pasture plots below the treeline is composed of sparse trees and grasses, whilst above the treeline pastures were dominated by grasses and lacked frailejones (Asteraceae: *Espeletiinae* subtribe), which are a cluster of highly endemic, slow-growing plant species with high sensitivity to disturbance and narrowly restricted geographical distribution (Cortés et al., 2018).

2.2. Sampling design

Orchid surveys were conducted from January 2019 to November 2020. Below the treeline, we randomly placed between 1 and 18 sampling plots keeping a minimum of 172 m distance apart (range = 172.3–2759 m, n = 148; Table S1). Larger natural and transformed areas had more plots to ensure broader coverage. All natural habitat plots were placed at least 30 m from the forest edge or roads. In the nearby transformed habitat, we established between 3 and 18 plots, located at least 60 m away from the forest edge and at a minimum of 193 m apart (range = 193–4225 m; n = 90 plots). Above the treeline, we randomly sampled plots in natural grasslands and shrublands, and high-elevation *Polylepis* forests, located at a minimum of 195 m apart (range = 195–15.170 m, n = 58). High-elevation transformed habitats consisted of pasturelands sampled at a minimum of 200 m apart (range = 200–4305 m, n = 45).

We sampled 206 natural habitats plots (148 forest, 48 paramo, and 10 paramo forest), and 135 transformed habitat plots (90 Andean transformed and 45 paramo transformed). We established a 10 × 30 m sampling plot within which we sampled all adult understory orchid individuals (Parra-Sanchez et al., 2023a). Thus, we had sampling plots of both natural and transformed habitats nested in the landscape (Fig. 1). Sampling substrates included the ground, standing tree trunks, fallen tree trunks and branches, vines, lianas, leaves on standing trees, herbaceous plants, palm trees, tree ferns, or cycads from the ground floor up to 2 m. We then recorded species and number of individuals (i.e., ramets). Ramets usually comprised various individual stems, but for our purpose, a ramet only counts as one single individual spatially separated from another set of stems of the same or another species (Sanford 1968). Identification to species or morphospecies was conducted following specialized literature and consultancy with local experts at the Herbarium VALLE. In the case of high levels of uncertainty in taxonomic identity, we morphotyped the species. All dubious individuals were placed in local nurseries for identification upon flowering. Species richness and the total number of individuals at each sampling plot were used as response variables.

2.3. Predictors

Elevation was taken in the field with a GPS garmin 60S device and later standardized with the ALOsPalsar terrain model by averaging the elevation within 50 m of the GPS point (Tadono et al., 2014). Precipitation (mean annual precipitation) was extracted at 1 km radius from each sampling plot from CHELSA (MAP; climatologies at high resolution for the Earth's land surface areas; Karger et al., 2020). Local habitat transformation was coded as binary factor, i.e., natural and transformed into pasturelands based on fieldwork.

2.4. Statistical analysis

We tested for independent, additive, and interactive effects between environmental variables and habitat transformation using GAMMs (General Additive Mixed Models). We assumed that an additive effect indicates the overall influence of both drivers as the sum of their individual effects, whereas a significant interaction effect shows that the effects of habitat transformation are modulated by the environment. General Additive Models deal with non-linear relationships between response and predictor variable, and nonparametric smoothers are used to describe the relationship (Wood, 2006). This model is suitable for any curved-shaped patterns, such as those along elevation gradients (Antonelli et al., 2018; Peters et al., 2019; Rahbek et al., 2019a).

We fit the models with observed species richness and abundance as response variables at plot level, and z-transformed all predictor variables before analyses, so that the model-averaged parameter estimates were standardized and centred to zero. GAMMs were sequentially fitted with elevation, precipitation, and local habitat treated as a dichotomous factorial variable (natural vs transformed habitat). We used Poisson error, or quasipoisson error distribution when Poisson models showed overdispersion, and used landscape as a random effect. We constrained our models to three or four knots (k = 3–4) to avoid overfitting, Restricted Maximum Likelihood (REML) was used as the estimation method, and the maximum number of PQL iterations was set at 30.

We tested four hypotheses. First, whether elevation or precipitation explain the variation in orchid diversity (species richness or abundance) across natural and transformed habitats (*environmental model*). Elevation and MAP were included as predictors and observed richness and total abundance as response variables (quassipoison family, and landscape as random effect). Second, that orchid diversity was best explained by the effect of the habitat transformation alone (*transformation model*). Models were fitted with local habitat transformation as the predictor, species richness and abundance as response variables, and landscape as a random effect. Third, that diversity was best explained by the effects of both habitat transformation and environment (the *additive model*: environment + transformation). Elevation, MAP, and local habitat transformation were included as additive predictors assuming that the whole effect of both sets of variables represents the sum of their individual effects. Finally, we tested the hypothesis that diversity was best explained by the interaction between habitat transformation and environment (the *interactive model*), assuming multiplicative effects of the environment and habitat transformation. Elevation × habitat transformation and MAP × habitat transformation were included as interaction terms.

Model performance was evaluated via inspection of the model diagnostic plots, r-squared (r2), and hanging rootograms ("appraise" and "rootograms" functions from gratia package). Rootograms are diagnostic tools that assess model goodness-of-fit, identifying whether observed frequencies match expected frequencies from the model

(Kleiber and Zeileis, 2016). In rootograms plots, expected counts (given the model) are shown by the thick continuous line, observed counts as bars hanging from the line of expected counts, the x-axis shows the count bin (0 count, 1 count, 2 count, etc.), the y-axis the square root of the observed or expected count, and finally a *reference* line is drawn at a height of 0 with its uncertainty (+/−1). In *hanging* rootogram, the model *over predicts* a particular bin when the bar does not reach the *reference* line (*observed* counts bin are shown as bars), whilst the model *under predicts* a particular bin if the bar exceeds the *reference* line (Kleiber and Zeileis, 2016).

2.5. Software

Statistical analyses were conducted using R 3.4.1 (R Core Team, 2022). Data formatting was performed via "tidyverse" package (Wickham et al., 2019), with GAMMs run using the "mgcv" package (Wood, 2017). Plots were elaborated in "ggplot" (Wickham, 2016) and "gratia" (Simpson Gavin, 2022).

3. Results

3.1. Species richness and abundance

We found 35,891 adult individuals of 331 species of which 91.6 % species are epiphytes (303 vs. 28 terrestrial species), with a maximum of 27 (range 0–27) species and 1012 (range 0–1012) individuals in a single plot (Supplementary material Table 1). We discovered several new species to science in both natural (Parra-Sanchez et al., 2023b; Parra-Sanchez et al., 2023c; Parra-Sanchez and Baquero, 2023) and transformed habitats (Ordóñez-Blanco and Parra-Sánchez, 2022).

3.2. Drivers of biogeographic patterns of orchid diversity in natural and transformed habitats

We found statistical support for all tested hypotheses. Environmental and land-use predictors showed significant results across models, with land-use consistently influencing orchid diversity negatively, although model performance varied.

Elevation and precipitation (*environmental model*) significantly impacted species richness (Fig. 2A, C) and total abundance (Fig. 2B, D). Both species richness (Fig. 2A; F-value = 21.98, p-value < 0.05; R-squared = −0.12) and abundance (Fig. 2B; F-value = 8.13, p-value < 0.05; R-squared = 0.12) peaked at mid-elevations (~2500 m) and then declined at around 3000 m. In contrast, precipitation showed a positive effect on species richness to ~1600 mm per year and level thereafter (Fig. 2C: F-value = 5.45; p-value < 0.05). Total abundance also revealed a positive effect of precipitation (to ~1800 mm per year) with a levelling thereafter until extreme values (>3300 mm per year), which caused a drop in abundance, although there was high uncertainty (Fig. 2D; F-value = 1.44, p-value = 0.24).

Land-use (*transformation model*) negatively influenced both species richness and total abundance (transformed habitat on richness, t-value

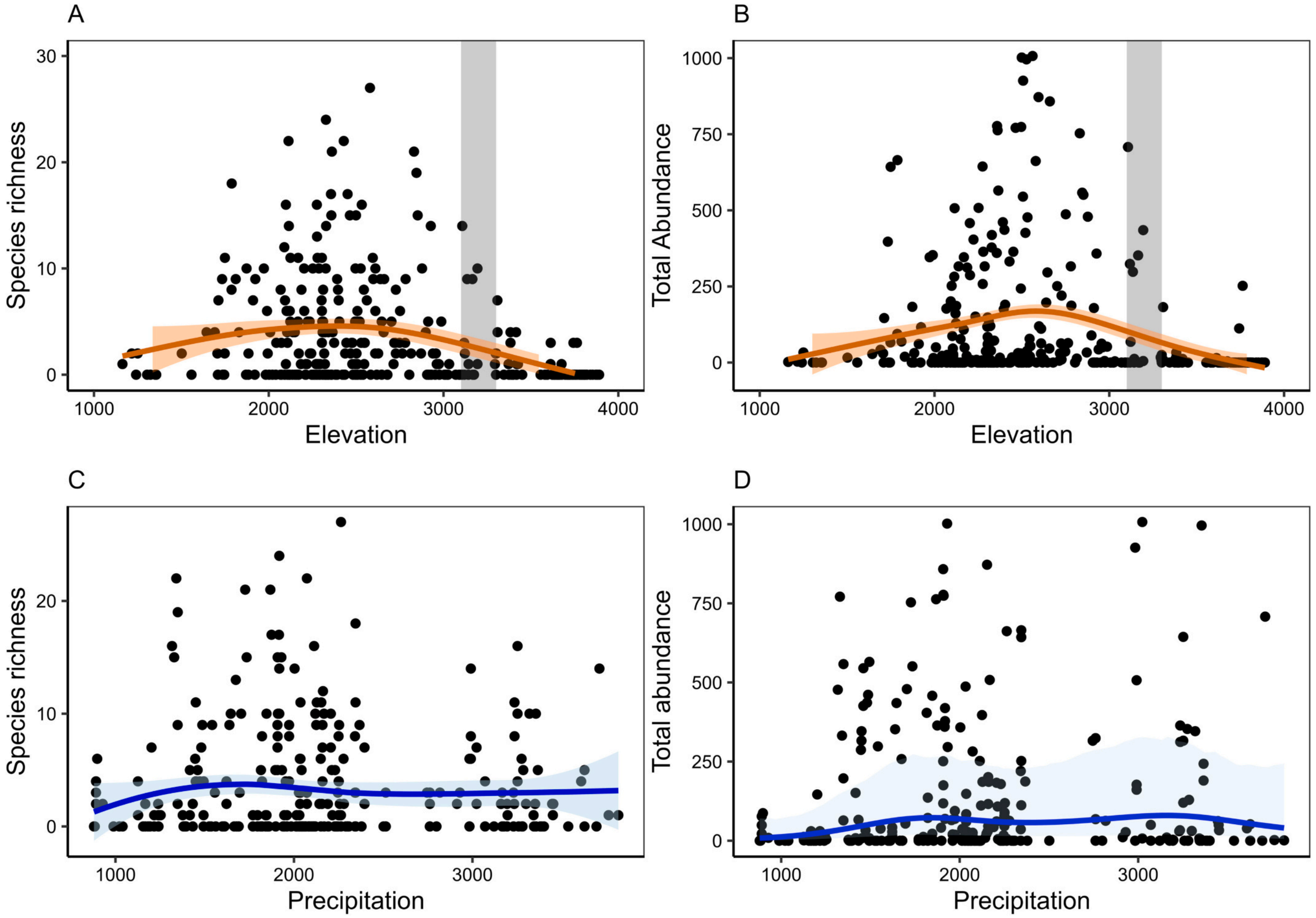

Fig. 2. Orchid species richness (A, C) and total abundance (B, D) along the elevational (in m.a.s.l.) and precipitation (in mm per year) gradient in the eastern Andes, Colombia. Plots depict the trend based on generalized additive models of species richness and total abundance (*environmental model*) for sampling plots (black dots), across the elevation (A–B) and precipitation (C–D) gradients. Grey shade shows the treeline's elevation cut-off. Shades along the trendline show the uncertainty (+/−0.05).

= −10.01; and abundance, t-value = −7.64; p-value< 0.05; R-squared = 0.18 and 0.14, respectively). Conversion of natural habitats to pasturelands resulted in substantial losses of orchid diversity, with ten-fold fewer species at the plot level (average 6.80 in natural vs 0.66 in transformed habitat; Fig. 3A, Table S2), equating to a 6-fold loss in overall species richness (300 vs 56), and 23-times fewer individuals (Fig. 3B; overall abundance = 31,256 vs 1434). Despite the low species richness in the transformed plots, 29 % of its species pool are endemic to Colombia and 37.4 % to the Andes, with one new species to science found in this habitat. Above the treeline, no orchids were found in the

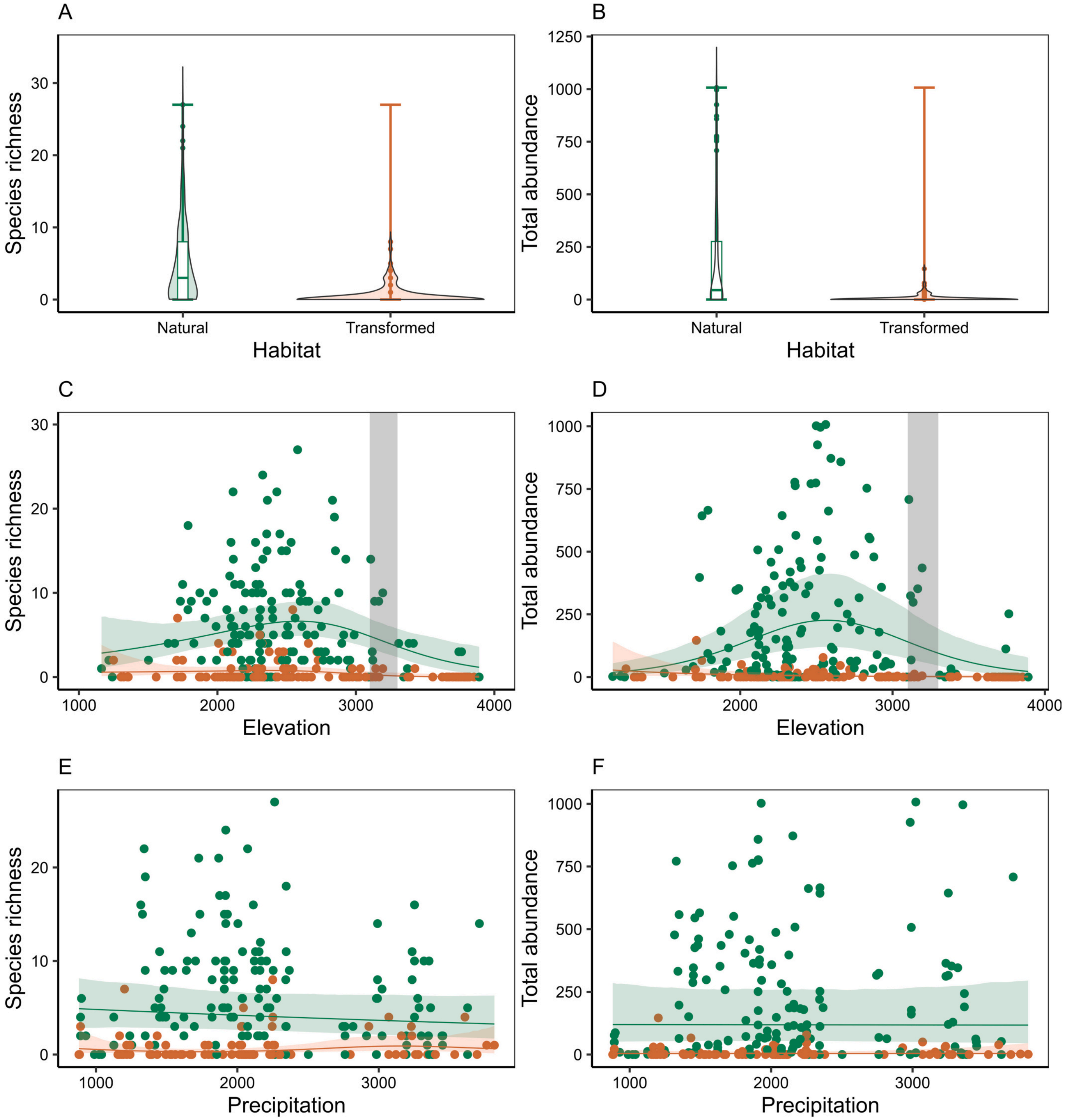

Fig. 3. Orchid species richness (A, C, E) and total abundance (B, D, F) along the land-use type and elevation (in m.a.s.l.) and precipitation (in mm per year) gradients in the eastern Andes, Colombia. Violin plots represent the effects of land-use on species richness (A) and total abundance (B) (transformation model), depicting the median value, and 25th and 75th percentile range for each land-use, the shaded area shows the kernel density of the variability range in natural (green) and transformed habitats (dark orange), whilst the circular dots represent the outliers in observed records of compositional turnover at each sampled plot. Trends are based on generalized additive models (GAMMs) testing for the effects of elevation by land-use (C,D) and precipitation by land-use (E,F), with shades along the trendline show uncertainty (Confidence intervals = +/−0.05). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

transformed habitats.

Conversion of natural habitats reconfigured the mid-elevation trend in orchid diversity pattern with elevation in natural habitat to a quasi-linear trend in transformed habitats that does not vary across elevation (Fig. 3C–D; Table S2). The positive influence of precipitation on orchid diversity seen in the *environment model* was also reshaped into a quasi-linear pattern in transformed habitats (Fig. 3E–F). The *additive* effects of environment + transformation influenced orchid species richness (Fig. 3C–E; elevation, F-value = 20.12; transformed habitat, t-value = −18.14; p-value < 0.05) and total abundance (Fig. 3D–F; elevation, F-value = 11.34; transformed habitat, t-value = −7.81; p-value < 0.05), whilst the additive effects of precipitation were negligible (richness, F-value = 3.35; abundance, F-value = 2.77; p-value > 0.10). Likewise, the *interactive* model (environment × transformation) displayed statistical support for the interaction between elevation and the natural habitat with species richness (F-value = 5.367, p-value < 0.05) and total abundance (chi-squared = 38.77, p-value < 0.05). Our model did not detect any significant interaction between our biogeographic drivers and the transformed habitat (p-value > 0.17), nor the interaction between precipitation and the natural habitat (p-value > 0.08).

In general, the *interactive*, *additive* (Fig. 4C) and, to a lesser degree, the *transformation* (Fig. 4; Fig. S1) models offered good statistical fit to our data (*interactive* R-squared = 0.182–0.401; *additive*, R-squared = 0.243–0.271; and *deforestation*, R-squared = 0.137–0.177). The *environment* model presented a lower goodness-of-fit (R-squared = 0.12; Fig. 4A). Despite the *interactive* model having better r-squared values, the *additive* model showed minimal deviations from the observed data in the lowest counts that would indicate over-prediction (i.e., Rootogram bins 1–3), the zero-count bin is better fitted, and most of the count bins fall within the reference lines, implying that the model did not under-predict observations (R2 > 0.162, Table S2).

4. Discussion

A key challenge is understanding how biogeographic patterns are impacted by conversion of natural habitats. Local-scale deforestation drives a severe loss of over 70 % of species richness and abundance in Andean orchid flora, and this conversion disrupts core biogeographic patterns of orchid diversity, rejecting our expectation. Our results highlight the importance of halting deforestation across environmental gradients, especially at elevations and precipitations where reshaping of biogeographic patterns maximises biodiversity loss.

4.1. Biogeographic patterns in natural habitat

Elevation and precipitation are important biogeographic forces of

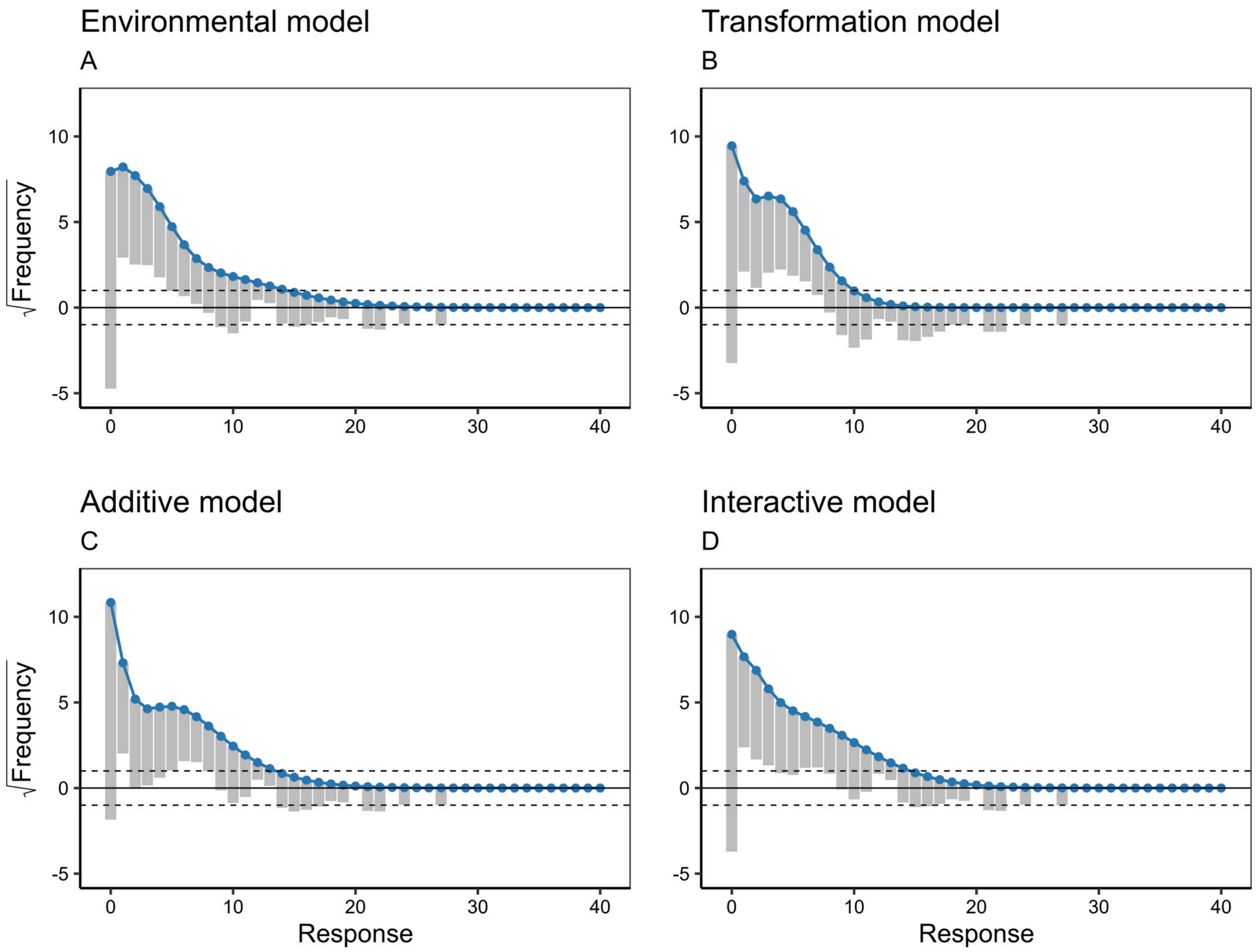

Fig. 4. Hanging Rootogram for illustrating the goodness-of-fit of each statistical hypotheses on species richness based on Generalized Additive Mixed Models (GAMMs). The x-axis represents the bin intervals of prediction errors, whilst the y-axis shows the frequency of occurrence. The expected counts, given by each model, are shown by the thick blue line, whilst observed counts are shown as bars, and the reference line is drawn at a height of 0 (±1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

orchid diversity. We found that orchid communities exhibit a mid-elevation diversity pattern across elevation in natural habitat, peaking at ~2500 m, which aligns with patterns for Andean trees and other epiphytic plants (Gentry and Dodson, 1987; Krömer et al., 2007; Malizia et al., 2020; Salazar et al., 2015; Santillán et al., 2018). Elevation relates to many other physical variables, such as topography, hydrologic regimes, and microclimatic factors, which might impact taxa that are drivers of orchid speciation and abundance, such as pollinators and mycorrhizae (Ackerman et al., 2023; Ramírez et al., 2011). For instance, most Andean bee species—one of the most important orchid pollinators—are restricted to Andean elevations between 1800 m and ~2400 m (Apidae and Halictidae, Gonzalez and Engel, 2007), although patterns of other orchid pollinators such as fungal gnats and dipterans (e.g. mosquitoes and flies Ackerman et al., 2023) are still unknown.

Precipitation drives high species richness at ~1800 mm per year and abundance at ~2000 mm per year, remaining constant thereafter. This finding aligns with local and regional patterns of rapid accumulation in species richness of vascular epiphytes at mid-precipitation, with a consistent and monotonically increasing trend as precipitation rises (Cardelus et al., 2006; Kreft et al., 2004; Krömer et al., 2013). Precipitation is an important driver of orchid diversity, with many epiphytic species drought-intolerant (Mondragon et al., 2014; Zotz, 2016) and precipitation promoting high diversity as seen in cloud forest (Pérez-Escobar et al., 2022; Tremblay, 1997b). We found that abundance fell at very high precipitation (>3300 mm per year), potentially because this reduces recruitment of wind-dispersed orchids (Mccall, 2007; Mondragon et al., 2014; Zuleta et al., 2016), although this pattern changes when accounting for land-use (see below).

4.2. *Impacts of local-scale habitat transformation on biogeographic patterns*

Habitat conversion exerts dramatic negative losses in orchid diversity and abundance—with >70 % of species and individuals lost below the treeline (~2900 m), and 100 % above the treeline—supporting findings from the Atlantic Forest (Parra-Sanchez and Banks-Leite, 2020), Venezuelan Andes (Barthlott et al., 2001), and Ecuador (Köster et al., 2009;but see Guzmán-Jacob et al., 2020, where alpha diversity of epiphytes did not differ significantly between natural and transformed habitats at low and high elevations). Habitat transformation also drives a fundamental reorganisation of the mid-elevation richness-elevation relationship to a quasi-linear trend in the transformed habitats, and of the positive effects of precipitation in natural habitats (higher richness and abundance in natural habitats, except >3300 mm per year), which became negligible following natural habitat transformation.

In contrast to our findings, the biodiversity-elevation trend between natural and transformed habitats converges at mid-elevations across taxa in Afromontane systems (Peters et al., 2019). This difference may reflect the presence of speciose communities evolved to live in more open-habitats at lower elevations that can invade mid-to higher-elevations in African mountains, versus the inherent dependency of orchid species to a host tree (96 % are epiphytes) and stable abiotic conditions within Andean forests (González del Pliego et al., 2016). Thus, many tropical orchids are pushed beyond their thermal limits (Acevedo et al., 2020) and drought tolerance after clearance (Mccall, 2007; Mondragon et al., 2014; Olaya-Arenas et al., 2011).

Whilst transformed habitats are unsuitable for most Andean orchids, nevertheless species endemic to Colombia and the Andes (29 % and 37.4 % of the total transformed species pool, respectively) were retained, as well as a new species to science (Ordóñez-Blanco and Parra-Sánchez, 2022). Whether transformed habitats can sustain these species long term is a key question. High seed mortality (estimated one individual survives *per* ~2000 seeds; Acevedo et al., 2020; Mondragon et al., 2014; Tremblay, 1997a), low demographic viability (Ospina-Calderón et al., 2023), dispersal limitation across landscapes, and high species turnover among and between habitats and elevations (Guzmán-Jacob et al., 2020; Parra-Sanchez et al., 2023a) might further exacerbate the effects of deforestation on orchids. Yet for other taxonomic groups, transformed habitats can offer some resources, serve as corridors for dispersion, or reproduction opportunities (Driscoll et al., 2013; Einzmann et al., 2021; Einzmann and Zotz, 2017b; Ramírez-Delgado et al., 2022). For instance, trees can serve as steeping stones to other species (Manning et al., 2006), whilst orchid bees are apparently insensitive to high levels of transformation because of their strong dispersal capabilities (Apidae, Crall et al., 2020; Nunes et al., 2022).

Our study has two key caveats. First, we focus on the lower part of the tree trunk, understory vegetation, and ground, which represents a subset of epiphyte species (Alzate-Q et al., 2019; Krömer et al., 2007) that may be particularly sensitive to change. Understory orchids are exposed to less microclimatic variability than tree crowns (Einzmann et al., 2021), which likely make the canopy more resilient to disturbance. Future research might cover entire trees, from understory to canopy, and further exploration of functional traits across large spatial scales could provide insight into the potential of species to respond to habitat transformation. Second, community-level metrics (i.e., richness and abundance) can be less sensitive to ecological processes than metrics that account for species turnover, via the loss of sensitive specialist species buffered to some extent by the arrival of generalist species (Larrea and Werner, 2010; Spake et al., 2022). Andean orchids exhibit high turnover across communities (Parra-Sanchez et al., 2023a, 2023b, 2023c), but the high net loss of orchid species and abundance provide strong evidence of the detrimental effects of habitat transformation.

5. Conclusions

Actions prioritizing the protection of highly diverse areas, in particular, where major losses of biodiversity can be averted are crucial. Our findings highlight elevations (~2500 m, mid-elevation) and precipitations (>1600 to <3300 mm/yr) where deforestation has the maximum negative impacts on orchid diversity. This suggests that practitioners should use our findings to guide locations at highest priority of protection from conversion, which is especially important given the international pledge at COP26 to establish new protected areas ('30 × 30'). It could also be used to target better placement of mandatory set-asides in Andean countries such as Ecuador and Colombia (República de Ecuador, Proyecto Socio Bosque (PSB), 2008; República de Colombia, Ley 388, 1997), so that neighbours form larger and better-connected set-aside forests, especially in mid-elevations and higher precipitation areas that can preserve higher orchid diversity.

Local-scale actions to retain and potentially restore orchid communities in mountainous regions also require improving landscape connectivity to facilitate orchid dispersal across human-modified landscapes, due to dispersal limitation (Parra-Sanchez et al., 2023a), and increase the likelihood of an influx of both epiphytic orchids and hosts (Einzmann and Zotz, 2017b; Mondragon et al., 2014; Zotz, 2016). We provide three recommendations to do so. First, retain tall trees in nearby natural habitat remnants as a source of forest trees, biomass, and epiphyte species (Wies et al., 2021; Woods et al., 2015). Second, allow growth of young trees near mature trees to boost the likelihood of occupancy by orchids (Richards et al., 2020) and hopefully to offset further loss of matrix trees (e.g., 141 trees disappeared of 763 surveyed over a span of 8-years in Panamanian lowlands; Einzmann and Zotz, 2017a, 2017b). Third, translocate adult orchid individuals between natural habitats and transformed habitats, which might enrich the matrix (Benavides et al., 2023; Reid et al., 2016). In conclusion, failure to adopt such approaches to prioritizing protected areas and improved connectivity will continue to exacerbate the dramatic loss of orchids and reshaping of core biogeographic patterns driven by habitat conversion.

Author statement

All authors wrote and approved the final version of this manuscript. We confirm that this work is original all done by the authors and is not currently being considered for publication elsewhere. During the preparation of this manuscript, we do not use AI or AI assisted technologies in the writing process and the authors take full responsibility for the content of the publication.

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CRediT authorship contribution statement

Edicson Parra-Sanchez: Writing – review & editing, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Robert P. Freckleton:** Writing – review & editing, Methodology, Formal analysis. **Matthew G. Hethcoat:** Writing – review & editing, Methodology. **Jose Manuel Ochoa-Quintero:** Writing – review & editing, Resources. **David P. Edwards:** Writing – review & editing, Visualization, Supervision, Resources, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data supporting the results of this study are available can be accessed via the following link: 10.6084/m9.figshare.23844138

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110538.

References

Acevedo, M.A., Beaudrot, L., Meléndez-Ackerman, E.J., Tremblay, R.L., 2020. Local extinction risk under climate change in a neotropical asymmetrically dispersed epiphyte. J. Ecol. 108 (4), 1553–1564. https://doi.org/10.1111/1365-2745.13361.

Ackerman, J.D., Phillips, R.D., Tremblay, R.L., Karremans, A., Reiter, N., Peter, C.I., Bogarín, D., Pérez-Escobar, O.A., Liu, H., 2023. Beyond the various contrivances by which orchids are pollinated: global patterns in orchid pollination biology. Bot. J. Linn. Soc. 202 (3), 295–324. https://doi.org/10.1093/botlinnean/boac082.

Alzate-Q, N.F., García-Franco, J.G., Flores-Palacios, A., Krömer, T., Laborde, J., 2019. Influence of land use types on the composition and diversity of orchids and their phorophytes in cloud forest fragments. Flora 260. https://doi.org/10.1016/j.flora.2019.151463.

Antonelli, A., Kissling, W.D., Flantua, S.G.A., Bermúdez, M.A., Mulch, A., Muellner-Riehl, A.N., Kreft, H., Linder, H.P., Badgley, C., Fjeldså, J., Fritz, S.A., Rahbek, C., Herman, F., Hooghiemstra, H., Hoorn, C., 2018. Geological and climatic influences on mountain biodiversity. Nat. Geosci. 11 (10), 718–725. https://doi.org/10.1038/s41561-018-0236-z.

Bader, M.Y., Rietkerk, M., Bregt, A.K., 2007. Vegetation structure and temperature regimes of tropical alpine treelines. Arct. Antarct. Alp. Res. 39 (3), 353–364. https://doi.org/10.1657/1523-0430(06-055)[BADER]2.0.CO;2.

Barthlott, W., Schmit-neuerburg, V., Nieder, J., Engwald, S., 2001. Diversity and abundance of vascular epiphytes: a comparison of secondary vegetation and primary montane rain forest in the Venezuelan Andes. Plant Ecol. 152, 145–156.

Benavides, A.M., Calderón-Caro, J., Canal, D., 2023. Surviving in a new host: eight years of monitoring translocated aroids, bromeliads, and orchids in the Andean forests in Colombia. Front. For. Glob. Change 6. https://doi.org/10.3389/ffgc.2023.834669.

Cardelus, C.L., Colwell, R.K., Watkins, J.E., 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. J. Ecol. 94 (1), 144–156. https://doi.org/10.1111/j.1365-2745.2005.01052.x.

Cortés, A.J., Garzón, L.N., Valencia, J.B., Madriñán, S., 2018. On the causes of rapid diversification in the Páramos: isolation by ecology and genomic divergence in *Espeletia*. Front. Plant Sci. 9 https://doi.org/10.3389/fpls.2018.01700.

Crall, J.D., Brokaw, J., Gagliardi, S.F., Mendenhall, C.D., Pierce, N.E., Combes, S.A., 2020. Wind drives temporal variation in pollinator visitation in a fragmented tropical forest. Biol. Lett. 16 (4), 20200103 https://doi.org/10.1098/rsbl.2020.0103.

Driscoll, D.A., Banks, S.C., Barton, P.S., Lindenmayer, D.B., Smith, A.L., 2013. Conceptual domain of the matrix in fragmented landscapes. Trends Ecol. Evol. 28 (10), 605–613. https://doi.org/10.1016/j.tree.2013.06.010.

Einzmann, H.J.R., Zotz, G., 2017a. Dispersal and establishment of vascular epiphytes in human-modified landscapes. AoB PLANTS 9 (6), 1–13. https://doi.org/10.1093/aobpla/plx052.

Einzmann, H.J.R., Zotz, G., 2017b. "No signs of saturation": long-term dynamics of vascular epiphyte communities in a human-modified landscape. Biodivers. Conserv. 26 (6), 1393–1410. https://doi.org/10.1007/s10531-017-1306-z.

Einzmann, H.J.R., Weichgrebe, L., Zotz, G., 2021. Long-term community dynamics in vascular epiphytes on *Annona glabra* along the shoreline of Barro Colorado Island, Panama. J. Ecol. 109 (4), 1931–1946. https://doi.org/10.1111/1365-2745.13618.

El Proyecto Socio Bosque (PSB). (2008).

Etter, A., Andrade, A., Saavedra, K., Amaya, P., Cortés, J., Arévalo, P., 2021. Ecosistemas colombianos: amenazas y riesgos. In: Una aplicación de la Lista Roja de Ecosistemas a los ecosistemas terrestres continentales. Pontificia Universidad Javeriana y Conservación Internacional-Colombia.

Ganuza, C., Redlich, S., Uhler, J., Tobisch, C., Rojas-Botero, S., Peters, M.K., Zhang, J., Benjamin, C.S., Englmeier, J., Ewald, J., Fricke, U., Haensel, M., Kollmann, J., Riebl, R., Uphus, L., Müller, J., Steffan-Dewenter, I., 2022. Interactive effects of climate and land use on pollinator diversity differ among taxa and scales. Sci. Adv. 8 (18) https://doi.org/10.1126/sciadv.abm9359.

Gentry, A., Dodson, C., 1987. Diversity and biogeography of neotropical vascular epiphytes. Ann. Mo. Bot. Gard. 74 (2), 205–233. http://www.jstor.org/stable/10.2307/2399395.

González del Pliego, P., Scheffers, B.R., Basham, E.W., Woodcock, P., Wheeler, C., Gilroy, J.J., Medina Uribe, C.A., Haugaasen, T., Freckleton, R.P., Edwards, D.P., 2016. Thermally buffered microhabitats recovery in tropical secondary forests following land abandonment. Biol. Conserv. 201, 385–395. https://doi.org/10.1016/j.biocon.2016.07.038.

Gonzalez, V.H., Engel, M.S., 2007. The tropical Andean bee fauna (Insecta: Hymenoptera: Apoidea), with examples from Colombia. Entomol. Abh. 62 (1), 65–75.

Gotsch, S.G., Nadkarni, N., Amici, A., 2016. The functional roles of epiphytes and arboreal soils in tropical montane cloud forests. J. Trop. Ecol. 32 (5), 455–468. https://doi.org/10.1017/S026646741600033X.

Guzmán-Jacob, V., Zotz, G., Craven, D., Taylor, A., Krömer, T., Monge-González, M.L., Kreft, H., 2020. Effects of forest-use intensity on vascular epiphyte diversity along an elevational gradient. Divers. Distrib. 26 (1), 4–15. https://doi.org/10.1111/ddi.12992.

Hu, Y., Gibson, L., Hu, H., Ding, Z., Zhou, Z., Li, W., Jiang, Z., Scheffers, B.R., 2022. Precipitation drives species accumulation whereas temperature drives species decline in Himalayan vertebrates. J. Biogeogr. https://doi.org/10.1111/jbi.14499.

Kala Rana, H., Kumar Rana, S., Luo, D., Sun, H., 2022. Existence of biogeographic barriers for the long-term Neogene-Quaternary divergence and differentiation of Koenigia forrestii in the Himalaya-Hengduan Mountains. Bot. J. Linn. Soc. 1–24. https://doi.org/10.1093/botlinnean/boac045/6883860.

Karger, D.N., Schmatz, D.R., Dettling, G., Zimmermann, N.E., 2020. High-resolution monthly precipitation and temperature time series from 2006 to 2100. Sci. Data 7 (1), 248. https://doi.org/10.1038/s41597-020-00587-y.

Karger, D.N., Kessler, M., Lehnert, M., Jetz, W., 2021. Limited protection and ongoing loss of tropical cloud forest biodiversity and ecosystems worldwide. Nat. Ecol. Evol. 5 (6), 854–862. https://doi.org/10.1038/s41559-021-01450-y.

Kleiber, C., Zeileis, A., 2016. Visualizing count data regressions using rootograms. Am. Stat. 70 (3), 296–303. https://doi.org/10.1080/00031305.2016.1173590.

Köster, N., Friedrich, K., Nieder, J., Barthlott, W., 2009. Conservation of epiphyte diversity in an Andean landscape transformed by human land use. Conserv. Biol. 23 (4), 911–919. https://doi.org/10.1111/j.15231739.2008.01164.x.

Kreft, H., Köster, N., Küper, W., Nieder, J., Barthlott, W., 2004. Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador. J. Biogeogr. 31, 1463–1476. http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2004.01083.x/full.

Krömer, T., Kessler, M., Robbert Gradstein, S., Acebey, A., 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. J. Biogeogr. 32 (10), 1799–1809. https://doi.org/10.1111/j.1365-2699.2005.01318.x.

Krömer, T., Kessler, M., Gradstein, S.R., 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecol. 189 (2), 261–278. https://doi.org/10.1007/s11258-006-9182-8.

Krömer, T., Acebey, A., Kluge, J., Kessler, M., 2013. Effects of altitude and climate in determining elevational plant species richness patterns: a case study from Los Tuxtlas, Mexico. Flora 208 (3), 197–210. https://doi.org/10.1016/j.flora.2013.03.003.

Larrea, M.L., Werner, F.a., 2010. Response of vascular epiphyte diversity to different land-use intensities in a neotropical montane wet forest. For. Ecol. Manag. 260 (11), 1950–1955. https://doi.org/10.1016/j.foreco.2010.08.029.

Ley 388 de 1997 (1997).

Lüttge, U., 1997. Páramos. In: Physiological Ecology of Tropical Plants. Springer, Berlin Heidelberg, pp. 349–371. https://doi.org/10.1007/978-3-662-03340-1_9.

Malizia, A.I., Blundo, C., Carilla, J., Osinaga Acosta, O., CuestaID, F., Duque, A., Aguirre, N., Aguirre, Z., Ataroff, M., Baez, S., Calderón-Loor, M., Cayola, L., Cayuela, L., Ceballos, S., Cedillo, H., Farfá Ríos, W., Feeley, K.J., Fernando Fuentes, A., Gámez A, L.E., Young, K.R., 2020. Elevation and Latitude Drives Structure and Tree Species Composition in Andean Forests: Results From a Large-scale Plot Network. https://doi.org/10.1371/journal.pone.0231553.

Manning, A.D., Fischer, J., Lindenmayer, D.B., 2006. Scattered trees are keystone structures - implications for conservation. Biol. Conserv. 132 (3), 311–321. https://doi.org/10.1016/j. biocon.2006.04.023.

Mccall, K., 2007. Precipitation variation and its effects on the reproductive success precipitation variation and its effects on the reproductive success and survival of Lepanthes jimenezii (Orchidaceae) and survival of Lepanthes jimenezii (Orchidaceae), University of South Florida. https://digitalcommons.usf.edu/tropical_ecology/547.

Mills, S.C., Socolar, J.B., Edwards, F.A., Parra, E., Martínez-Revelo, D.E., Ochoa Quintero, J.M., Haugaasen, T., Freckleton, R.P., Barlow, J., Edwards, D.P., 2022. High sensitivity of tropical forest birds to deforestation at lower altitudes. Ecology. https://doi.org/10.1002/ecy.3867.

Mondragon, D., Valverde, T., Hernandez, M., 2014. Population ecology of epiphytic angiosperms: a review. Trop. Ecol. 56 (1), 01–39. https://doi.org/10.13140/2.1.4043.5849.

Nunes, C.A., Berenguer, E., França, F., Ferreira, J., Lees, A.C., Louzada, J., Sayer, E.J., Solar, R., Smith, C.C., Aragão, L.E.O.C., Braga, D. de L., de Camargo, P.B., Cerri, C.E. P., de Oliveira, R.C., Durigan, M., Moura, N., Oliveira, V.H.F., Ribas, C., Vaz-de-Mello, F., Barlow, J., 2022. Linking land-use and land-cover transitions to their ecological impact in the Amazon. Proc. Natl. Acad. Sci. 119 (27) https://doi.org/10.1073/pnas.2202310119.

Olaya-Arenas, P., Meléndez-Ackerman, E.J., Pérez, M.E., Tremblay, R., 2011. Demographic response by a small epiphytic orchid. Am. J. Bot. 98 (12), 2040–2048. https://doi.org/10.3732/ajb.1100223.

Ordóñez-Blanco, J.C., Parra-Sánchez, E., 2022. Small-flowered *Cyrtochilum* (Oncidiinae) from Colombia. Lankesteriana 22 (3), 207–214. https://doi.org/10.15517/lank.v22i3.52974.

Ospina-Calderón, N.H., Tremblay, R.L., Torres, A.M., Flanagan, N.S., 2023. The effect of habitat transformation on a twig epiphytic orchid: evidence from population dynamics. Front. Ecol. Evol. 11 https://doi.org/10.3389/fevo.2023.1135316.

Parra-Sanchez, E., Banks-Leite, C., 2020. The magnitude and extent of edge effects on vascular epiphytes across the Brazilian Atlantic Forest. Sci. Rep. 10 (1), 18847 https://doi.org/10.1038/s41598-020-75970-1.

Parra-Sanchez, E., Banks-Leite, C., 2022. Value of human-modified forests for the conservation of canopy epiphytes. Biotropica. https://doi.org/10.1111/btp.13119.

Parra-Sanchez, E., Baquero, L., 2023. Circumscription, first confirmed locality, and conservation status of *Dracula anthracina* (Orchidaceae). Syst. Bot. 48 (2), 200–207. https://doi.org/10.1600/036364423X16847773873080.

Parra-Sanchez, E., Pérez-Escobar, O.A., Edwards, D.P., 2023a. Neutral-based processes overrule niche-based processes in shaping tropical montane orchid communities across spatial scales. J. Ecol. https://doi.org/10.1111/1365-2745.14140.

Parra-Sanchez, E., Restrepo, E., Alegria-Valencia, M., Moreno, J.S., Galindo-Tarazona, R., 2023b. *Lepanthes cordillerana* (Orchidaceae) a new species and the landscape threats to its wild populations. Phytotaxa 603 (1), 69–80. https://doi.org/10.11646/phytotaxa.603.1.5.

Parra-Sanchez, E., Vieira-Uribe, S., Moreno, J.S., 2023c. New species of *Lepanthes* (Orchidaceae: Pleurothallidinae) to honour "Bachué", the mythological mother of the indigenous Muisca people. Lankesteriana 23 (2). https://doi.org/10.15517/lank.v23i2.54032.

Pérez-Escobar, O.A., Chomicki, G., Condamine, F.L., Karremans, A.P., Bogarín, D., Matzke, N.J., Silvestro, D., Antonelli, A., 2017. Recent origin and rapid speciation of Neotropical orchids in the world's richest plant biodiversity hotspot. New Phytol. 215 (2), 891–905. https://doi.org/10.1111/nph.14629.

Pérez-Escobar, O.A., Zizka, A., Bermúdez, M.A., Meseguer, A.S., Condamine, F.L., Hoorn, C., Hooghiemstra, H., Pu, Y., Bogarín, D., Boschman, L.M., Pennington, R.T., Antonelli, A., Chomicki, G., 2022. The Andes through time: evolution and distribution of Andean floras. In: Trends in Plant Science, vol. 27 (4). Elsevier Ltd., pp. 364–378. https://doi.org/10.1016/j.tplants.2021.09.010

Peters, M.K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Haas, M., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Mwangomo, E., Ngereza, C., Otte, I., Röder, J., Rutten, G., Steffan-Dewenter, I., 2016. Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nat. Commun. 7 https://doi.org/10.1038/ncomms13736.

Peters, M.K., Hemp, A., Appelhans, T., Becker, J.N., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S.W., Frederiksen, S.B., Gebert, F., Gerschlauer, F., Gütlein, A., Helbig-Bonitz, M., Hemp, C., Kindeketa, W.J., Kühnel, A., Mayr, A.v., Mwangomo, E., Steffan-Dewenter, I., 2019. Climate–land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568 (7750), 88–92. https://doi.org/10.1038/s41586-019-1048-z.

R Core Team, 2022. R: a language and environment for statistical. In: R Foundation for Statistical Computing.

Rahbek, C., Borregaard, M.K., Antonelli, A., Colwell, R.K., Holt, B.G., Nogues-Bravo, D., Rasmussen, C.M.Ø., Richardson, K., Rosing, M.T., Whittaker, R.J., Fjeldså, J., 2019a. Building mountain biodiversity: geological and evolutionary processes. In: Science, vol. 365 (6458). American Association for the Advancement of Science, pp. 1114–1119. https://doi.org/10.1126/science.aax0151.

Rahbek, C., Borregaard, M.K., Colwell, R.K., Dalsgaard, B., Holt, B.G., Morueta-Holme, N., Nogues-Bravo, D., Whittaker, R.J., Fjeldså, J., 2019b. Humboldt's enigma: what causes global patterns of mountain biodiversity? Science 365 (6458), 1108–1113. https://doi.org/10.1126/science.aax0149.

Ramírez, S.R., Eltz, T., Fujiwara, M.K., Gerlach, G., Goldman-Huertas, B., Tsutsui, N.D., Pierce, N.E., 2011. Asynchronous diversification in a specialized plant-pollinator mutualism. Science 333 (6050), 1742–1746. https://doi.org/10.1126/science.1209175.

Ramírez-Delgado, J.P., Di Marco, M., Watson, J.E.M., Johnson, C.J., Rondinini, C., Corredor Llano, X., Arias, M., Venter, O., 2022. Matrix condition mediates the effects of habitat fragmentation on species extinction risk. Nat. Commun. 13 (1) https://doi.org/10.1038/s41467-022-28270-3.

Reid, J.L., Chaves-Fallas, J.M., Holl, K.D., Zahawi, R.A., 2016. Tropical forest restoration enriches vascular epiphyte recovery. Appl. Veg. Sci. 19 (3), 508–517. https://doi.org/10.1111/avsc.12234.

Richards, J.H., Torrez Luna, I.M., Waller, D.M., 2020. Tree longevity drives conservation value of shade coffee farms for vascular epiphytes. Agric. Ecosyst. Environ. 301, 107025 https://doi.org/10.1016/j.agee.2020.107025.

Rodríguez Eraso, N., Armenteras-Pascual, D., Alumbreros, J.R., 2013. Land use and land cover change in the Colombian Andes: dynamics and future scenarios. J. Land Use Sci. 8 (2), 154–174. https://doi.org/10.1080/1747423X.2011.650228.

Salazar, L., Homeier, J., Kessler, M., Abrahamczyk, S., Lehnert, M., Krömer, T., Kluge, J., 2015. Diversity patterns of ferns along elevational gradients in Andean tropical forests. Plant Ecol. Divers. 8 (1), 13–24. https://doi.org/10.1080/17550874.2013.843036.

Santillán, V., Quitián, M., Tinoco, B.A., Zárate, E., Schleuning, M., Böhning-Gaese, K., Neuschulz, E.L., 2018. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient. PLoS ONE 13 (5). https://doi.org/10.1371/JOURNAL.PONE.0196179.

Simpson Gavin, 2022. Package 'gratia'-based graphics and other functions for GAMs fitted using "mgcv". https://orcid.org/0000-0002-4842-3657.

Spake, R., Barajas-Barbosa, M.P., Blowes, S.A., Bowler, D.E., Callaghan, C.T., Garbowski, M., Jurburg, S.D., Van Klink, R., Korell, L., Ladouceur, E., Rozzi, R., Viana, D.S., Xu, W.-B., Chase, J.M., 2022. Detecting Thresholds of Ecological Change in the Anthropocene. https://doi.org/10.1146/annurev-environ-112420.

Tadono, T., Ishida, H., Oda, F., Naito, S., Minakawa, K., Iwamoto, H., 2014. Precise global DEM generation by ALOS PRISM. In: ISPRS Annals of the Photogrammetry, Remote Sensing and Spatial Information Sciences, II–4, pp. 71–76. https://doi.org/10.5194/isprsannals-II-4-71-2014.

Tolmos, M.L., Kreft, H., Ramirez, J., Ospina, R., Craven, D., 2022. Water and energy availability mediate biodiversity patterns along an elevational gradient in the tropical Andes. J. Biogeogr. 49 (4), 712–726. https://doi.org/10.1111/jbi.14332.

Tremblay, R.L., 1997a. Distribution and dispersion patterns of individuals in nine species of *Lepanthes* (Orchidaceae). Biotropica 29 (1), 38–45. https://doi.org/10.1111/j.1744-7429.1997.tb00004.x.

Tremblay, R.L., 1997b. Distribution and dispersion patterns of individuals in nine species of *Lepanthes* (Orchidaceae). Biotropica 29 (1), 38–45.

Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L.E.O.C., Nasi, R., 2021. Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. Sci. Adv. 7 (10) https://doi.org/10.1126/sciadv.abe1603.

Wickham, H., 2016. ggplot2: elegant graphics for data analysis, Springer-Verlag. ggplot2.tidyverse.org.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T., Miller, E., Bache, S., Müller, K., Ooms, J., Robinson, D., Seidel, D., Spinu, V., Yutani, H., 2019. Welcome to the Tidyverse. J. Open Source Softw. 4 (43), 1686. https://doi.org/10.21105/joss.01686.

Wies, G., Nicasio Arzeta, S., Martinez Ramos, M., 2021. Critical ecological thresholds for conservation of tropical rainforest in Human Modified Landscapes. Biol. Conserv. 255 https://doi.org/10.1016/j.biocon.2021.109023.

Wilson, A.M., Jetz, W., 2016. Remotely sensed high-resolution global cloud dynamics for predicting ecosystem and biodiversity distributions. PLoS Biol. 14 (3), e1002415 https://doi.org/10.1371/journal.pbio.1002415.

Wood, S.N., 2006. Generalized Additive Models: An Introduction With R. Chapman & Hall and CRC.

Wood, S.N., 2017. Generalized additive models: an introduction with R, second edition. In: Generalized Additive Models: An Introduction With R, Second Edition. CRC Press. https://doi.org/10.1201/9781315370279.

Woods, C.L., Cardelús, C.L., Dewalt, S.J., 2015. Microhabitat associations of vascular epiphytes in a wet tropical forest canopy. J. Ecol. 103 (2), 421–430. https://doi.org/10.1111/1365-2745.12357.

Wraith, J., Pickering, C., 2018. Quantifying anthropogenic threats to orchids using the IUCN Red List. Ambio 47 (3), 307–317. https://doi.org/10.1007/s13280-017-0964-0.

Zotz, G., 2016. Plants on Plants – The Biology of Vascular Epiphytes. Springer International Publishing.

Zuleta, D., Benavides, A.M., López-Rios, V., Duque, A., 2016. Local and regional determinants of vascular epiphyte mortality in the Andean mountains of Colombia. J. Ecol. 104 (3), 841–849. https://doi.org/10.1111/1365-2745.12563.