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RESEARCH ARTICLE

Spatial extent predicts Andean epiphyte biodiversity responses to habitat loss and fragmentation across human-modified landscapes

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Abstract

Aim: Human-driven landscape processes such as habitat loss and fragmentation act on biodiversity, but their effects are mediated by the spatial scale at which they are observed. We aim to analyse the scale-of-effects (direction and spatial extent) of landscape-scale processes that best explain species richness and abundance across epiphyte communities.

Location: Neotropics, Northern Andes, Colombia, Eastern cordillera.

Taxon: Vascular epiphytes, Orchidaceae.

Methods: We used field data to unravel the scale-of-effect of three landscape processes—habitat loss (forest cover), fragmentation (number of patches) and edge effects (edge density)—on epiphyte biodiversity. Vascular epiphytes were sampled in the understorey across 141 plots within 23 Andean forests in the eastern Colombian cordillera We focused on the community-level responses (species richness and total abundance) of the hyperdiverse vascular epiphyte communities using generalized linear mixed models to quantify the direction and the spatial extent of the scale-of-effects.

Results: Habitat loss and edge effects act at fine spatial extents (scale-of-effects = 200 m), predicting low species richness and abundance across groups. Likewise, fragmentation negatively impacts communities, but operates at larger spatial extents (scale-of-effects = 2000–2400 m radius). The detection of these effects is contingent upon the spatial extent and specific landscape processes involved. Models of habitat loss within a spatial extent of 800–1500 m (large confidence intervals), fragmentation below 300 m, and edge effects above 800 m show weak statistical support (marginal r^2 = 0.02–0.1). Thus, the impacts of these landscape processes may be overlooked if studied at inadequate spatial extents.

Main Conclusions: We showed that habitat loss, fragmentation and edge effects all play a negative role on understorey epiphytic communities, but their detectability is scale dependant. The scale-of-effects can assist landscape designs that are beneficial for epiphytic communities, by preserving forest cover, and reducing fragmentation and exposure to edge effects at small scales (200–300 m). Conversely, landscape-scale actions directed at reducing habitat loss and fragmentation function at larger

spatial extents (>2000 m). Selecting a priori or inadequate spatial extents of analysis can obscure the detectability of landscape processes.

KEYWORDS

community ecology, fragmentation, habitat loss, landscape ecology, orchids, tropical Andes, understorey

1 | INTRODUCTION

Ecological patterns and processes are inherently scale dependent (Levin, 1992; Wiens, 1989). Failing to quantify the spatial scale at which biodiversity patterns and processes are shaped can lead to incorrect quantification of their impacts and potentially in-effective conservation strategies in a human-dominated world (Arroyo-Rodríguez et al., 2020). Detectability of this spatial scale is important because populations, species and communities use, interpret and respond to their habitats and surroundings in different ways. For instance, the average spatial extents at which species have the strongest relationship with landscape drivers is 1000 m, but its extent ranged from 40 m to 5500 m, making it highly taxa and context dependent (Saura, 2020). Although the importance of spatial scale and the role of the landscape on shaping biodiversity is well-acknowledged (Arroyo-Rodríguez et al., 2020; Jackson & Fahrig, 2015; Turner et al., 1989), our understanding of their effects and consequences on plant biodiversity is still poor across mountainous landscapes.

Mountain ecosystems are one of the richest biodiversity hotspots worldwide, but they have been severely transformed by human activities (Rahbek et al., 2019; Vancutsem et al., 2021). For instance, the Northern Andes ranks first in diversity of birds, butterflies and plants (Myers et al., 2000; Pérez-Escobar et al., 2022), but less than 40% of its natural landscape remains (Rodríguez Eraso et al., 2013). In general, once the natural landscape is transformed by human activities, three main landscape processes appear: (1) habitat loss or the decline of suitable habitat in terms of area (Ewers & Didham, 2008; Fahrig, 2003); (2) fragmentation as the physical partitioning of the landscape into smaller pieces (Fahrig, 2003, 2017); and (3) edge effects from the creation of new edges between two or more habitats (Malcolm, 1994; Ries et al., 2017). The effects of these landscape processes are highly context-dependent because evidence has shown negative, positive, neutral and interactive effects.

Habitat loss is consistently the strongest landscape process on species richness, with negative effects across taxa, scales and response metrics (Arroyo-Rodríguez et al., 2020; Fahrig, 2017; Saura, 2020), to the point of threatening species' populations with extinction (Brooks et al., 2002). In contrast, fragmentation studies have shown positive, neutral and negative effects on biodiversity (Arroyo-Rodríguez & Dias, 2010; Fletcher et al., 2018; Gestich et al., 2019). A multiscale study across the Brazilian Atlantic Forest shows that fragmentation negatively affects species richness (flora and fauna), but the strength of impact is modulated by forest cover

in the landscape (Püttker et al., 2020). Edge effects also have several negative impacts on plant diversity including the reduction of forest-dependent species (Parra-Sánchez et al., 2016; Püttker et al., 2020). However, the detectability of the direction and extension of these landscape processes relies on the spatial extent ('scale-of-effects').

The scale-of-effects is a concept that seeks to unravel the most informative spatial extent at which the effect of a particular landscape process is detectable and relevant for biodiversity (Fahrig, 2013; Jackson & Fahrig, 2015). Investigating the scale-of-effects requires understanding of the spatial grain and spatial extent. The spatial grain determines the smallest unit of analysis, which in scale-of-effects studies is the sampling plot where the targeted taxa and metrics are collected (Turner et al., 1989; McGarigal et al., 2009). The spatial extent refers to the overall geographic scope of the study area, encompassing the boundaries within which data are analysed (McGarigal et al., 2009; Turner et al., 2001). In scale-of-effects studies, the spatial extent progressively varies in area to find the most relevant scale, using concentric extents centred at the grain (i.e. sample plot) to quantify the effects of landscape process on biodiversity (Jackson & Fahrig, 2015). By further expanding the concept, scale-of-effects can also inform the magnitude and direction of the correlation, which provides insights into the impact (positive, negative, neutral or not detected) that the landscape process has on biodiversity.

The quantification of the scale-of-effects moves beyond a purely ecological-methodological concern, towards a pragmatic tool that could improve the successful implementation of conservation strategies such as land-sharing/land-sparing actions (Fischer et al., 2014) and restoration initiatives (Crouzeilles & Curran, 2016), by detecting the spatial extent and direction of the effects of human activity on biodiversity. For instance, a global meta-analysis found that successful biodiversity outcomes following forest restoration are best predicted by the amount of forest cover present within a 5–10-km radius (Crouzeilles & Curran, 2016). Therefore, understanding of this scale-dependent response can help target effective restoration (Brancalion et al., 2019).

Scale-of-effects studies on plant species richness point to negative effects of habitat loss within 1500–2000 m in the Brazilian Atlantic Forest (Püttker et al., 2020), but no effect at fine spatial extents within 50–650 m in Costa Rica (Holl et al., 2017). While fragmentation shows a reduction of species richness at spatial extents of 1800–2000 m, its effects are associated with edge effects (Püttker et al., 2020). In Mexico, edge density negatively affects seedling richness within 50–1000 m, but fragmentation exerts no effects

(San-José et al., 2020). These studies demonstrate the need to empirically quantify the scale-of-effects (Arroyo-Rodríguez et al., 2020; Jackson & Fahrig, 2015). As we quantify the scale-of-effects on different taxa and ecosystems, new patterns might emerge, especially because data collection is often systematically, geographically or taxonomically biased, which could bias predictions, especially for rare taxa in human-modified landscapes (Fardila et al., 2017; Trimble & van Aarde, 2012).

We focus our study on understorey vascular epiphytes, that is, non-soil rooted vascular plants that live on a host without parasitizing them (Zotz, 2013). This group represents 10% of the global vascular flora (Taylor et al., 2021; Zotz, 2013), yet epiphytes are usually underrepresented in multiscale studies. Vascular epiphytes have several attributes that in combination make them an interesting group for quantifying the impacts of habitat loss and fragmentation and the spatial extent at which they best predict biodiversity. These attributes include: high taxonomical diversity; species with high specialization; high mortality rate (four times higher than soil-rooted plants; Zuleta et al., 2016); potential dispersal limitation (Janzen et al., 2020); large numbers of threatened species (Calderón-Saenz, 2007); high interspecies-ecological equivalence (Catchpole & Kirkpatrick, 2010); and low-to-negligible interspecific competition (Zotz, 2016). At local scale, large trees support higher epiphyte diversity than smaller trees, and trees with complex crowns support more epiphytes than trees with simple crown structure (Woods et al., 2015; Zuleta et al., 2016). In contrast, remnant trees often host vascular epiphytes in their crowns (Einzmann & Zotz, 2017a, 2017b). However, the scale-of-effects of habitat loss, fragmentation, and edge effects have not been quantified on vascular epiphytes leaving a big gap in our understanding of the appropriate scale for landscape management of this speciose group (Flores-Palacios & García-Franco, 2007; Hernandez-Perez & Solano, 2015; Köster et al., 2009; Larrea et al., 2010; Parra-Sanchez & Banks-Leite, 2020; Ruete et al., 2018; Zuleta et al., 2016).

We aim to analyse the scale-of-effects (direction and spatial extent) of landscape-scale processes that best explain understorey species richness and abundance across epiphyte communities by specifically asking: (1) what is the direction and the spatial extent at which habitat loss best explain epiphyte communities; and (2) what is the direction and the spatial extent at which fragmentation and edge effects best explain epiphyte communities? Our first expectation focuses on the positive correlation of epiphyte diversity with forest cover, regardless of the spatial extent, because forest cover promotes resource availability and landscape connectivity (Arroyo-Rodríguez et al., 2020). Our second expectation lies in the consistent negative effects of habitat fragmentation and edge effects on epiphyte diversity irrespective of the spatial extent, due to the high habitat specialization, potential dispersal limitation in epiphyte communities and sensitivity to environmental changes caused by habitat loss and fragmentation (Janzen et al., 2020; Werner, 2011; Zotz, 2005; Zuleta et al., 2016). Our third expectation is that effects might be different for orchids acting at low spatial extents versus other epiphytes, due to the sensitivity of orchids to local disturbance reflected in altered species densities, high compositional turnover in the Andes, and high proportion of orchid species threatened with extinction relative to any other epiphytic family (Carmona-Higuita et al., 2023; Parra-Sanchez et al., 2023; Parra-Sánchez et al., 2016).

2 | MATERIALS AND METHODS

The study was located in the departments of Cundinamarca, Boyacá, Meta and Santander, in the Colombian eastern cordillera (Figures 1 and 2). We sampled 23 forests across a wide elevational range (1163–3415 m) belonging to the Andean mountains (Pérez-Escobar et al., 2022), with mean cloud cover of 82% (25–90%; Wilson & Jetz, 2016), temperature ranging 7–28°C and annual precipitation of 891–3711 mm per year. Andean forests were randomly selected based on forest availability in the area, logistic constraints (accessibility, permit from landowners, topography), and safety and security considerations. We randomized forest selection because forests at both extremes of the gradient are scarce either due to deforestation (<1400 m; Aide et al., 2019), or natural absence above the treeline (>3000 m; Bader et al., 2007; Lüttge, 1997). Forest belonged to two types: Andino (21 forests) and Altoandino (2) (Etter et al., 2021; Table S1). Forests had discrete boundaries surrounded by a predominantly pastureland matrix. Although all sampled sites belonged to the network of protected areas in Colombia (Sistema nacional de areas protegidas, SINAP), we considered them as having undergone low-intensity human-induced modification, given the easy accessibility by roads or footpaths, selective logging for local uses and knowledge from local field assistants.

2.1 | Sampling

Surveys were conducted from January to November 2019 following Parra-Sanchez et al. (2023). We sampled between 2 and 18 sampling plots in the understorey of 10×30 m in each forest (*n* = 141). Larger forest areas had more plots to ensure wider coverage. Sampling plots were randomly placed in sections of the forest at least 30 m from edges to reduce the effects of cattle movement and grazing (*pers. obser.* and Parra-Sánchez et al., 2016). Sampling plots were located between 150 and 600 m apart inside each forest. This design allows us to capture a large variability of species richness and high turnover across communities (Parra-Sanchez et al., 2023).

We recorded all individuals on standing tree trunks, fallen tree trunks and branches, vines, lianas, leaves on standing trees or herbaceous plants, palm trees, tree ferns and cycads without soil contact in the understorey. The operational concept of understorey we used was the section of the forest between 50 and 200 cm aboveground, where it is expected to have lower light levels, reduced wind exposure and greater humidity compared to the upper canopy (Coenders-Gerrits et al., 2020; Ewers & Banks-Leite, 2013). The number of species and adult individuals (i.e. ramets) were recorded, while younger stages were not included due to a large uncertainty
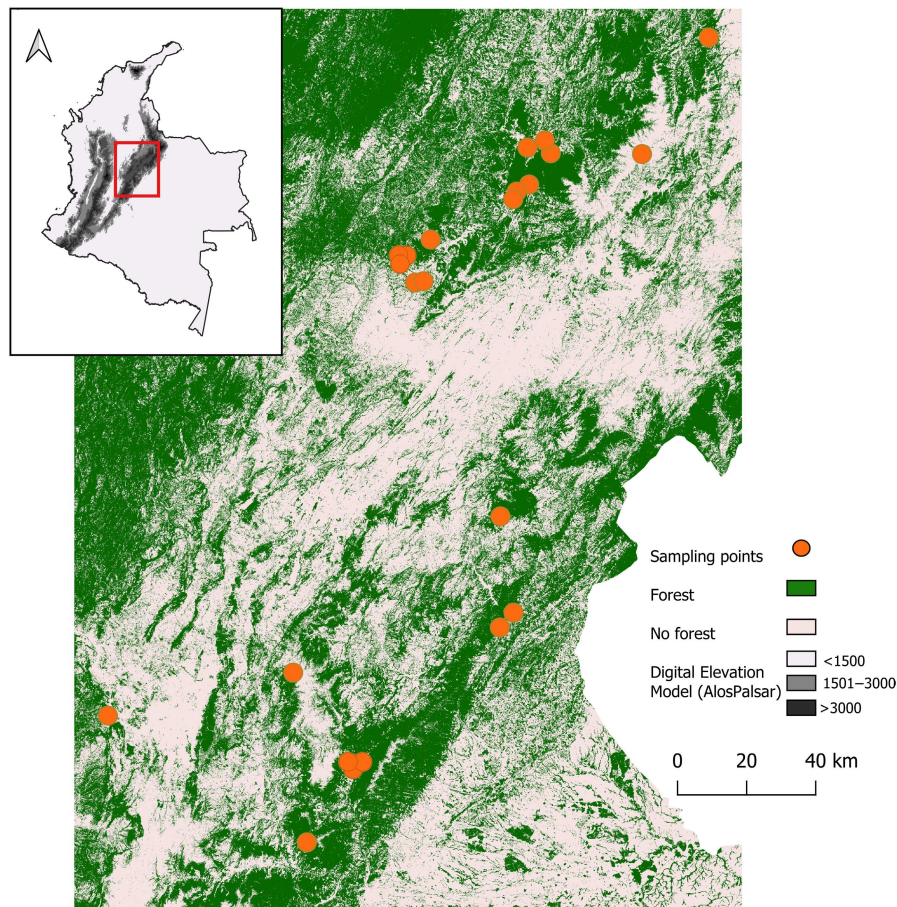
FIGURE 1 Sampling points of epiphytic communities across the eastern cordillera in Colombia (WGS84). Centroid of the focal Andean Forest fragments (in orange, $n = 23$), their respective surrounding forest (black) and non-forest (grey), and AlosPalsar Digital Elevation model (Tadono et al., 2014).

in species identification. 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, or an empty space (Sanford, 1968). Adult plants were defined as all large individuals (within the observed variation in the local population) with evidence of developed floral or reproductive structure, large ramets, many stems per stand and a prominent root system.

Identification to species or morphospecies was conducted following specialized literature and expertise of local experts at the Herbarium VALLE. Orchid species with no flowers were taken to nurseries in the vicinity of the sampled plots, and later visited for identification. All dubious individuals and juveniles were ignored due to uncertainty in their taxonomical rank.

2.2 | Response variables

We used observed values of species richness and total abundance per plot for the two groups: orchids and non-orchid epiphytes (hereafter NOE; including Bromeliaceae, Gesneriaceae, Araceae and ferns). We focused on orchids as the most species-rich epiphytic family (Zotz 2021), dominant Andean plant family (Pérez-Escobar et al., 2022), its high sensitivity to forest disturbance and edge effects (Parra-Sanchez & Banks-Leite, 2020) and higher proportion

of species threatened with extinction than other epiphytic families (Carmona-Higuita et al., 2023). We identified 82.2% of orchid plants to species level (273 species) and the remaining 17.8% plants to morphotypes (59 spp). For all NOE, we morphotyped each species at the plot level due to the impossibility of obtaining enough diagnostic characters and high levels of uncertainty in taxonomic identity across plots, resulting in a species richness count per plot. Therefore, analyses used the total number of species and morphospecies for orchids, and only morphospecies at plot level of NOE.

2.3 | Environmental predictors

We calculated landscape metrics at twelve arbitrary selected spatial extents centred on the sampling plot, thus: buffers of 100, 200, 300, 500, 800, 1000, 1200, 1500, 1800, 2000, 2200 and 2400 m (Figure 2). The landscape metrics capture high variability across the range of spatial extents (Figure S1). We included a wide range of spatial extents because the dispersal of epiphyte species varies from a few meters to long distance. Epiphytic plants have large dispersal kernels that allow them to cross fragmented habitats (Einzmann & Zotz, 2017a, 2017b; Mondragón et al., 2015), although other wind-dispersed seeds from epiphytic bromeliads and orchid species land very closely to their source <10 m (Mondragón et al., 2015; Mondragon & Calvo-Irabien, 2006). The grain of the
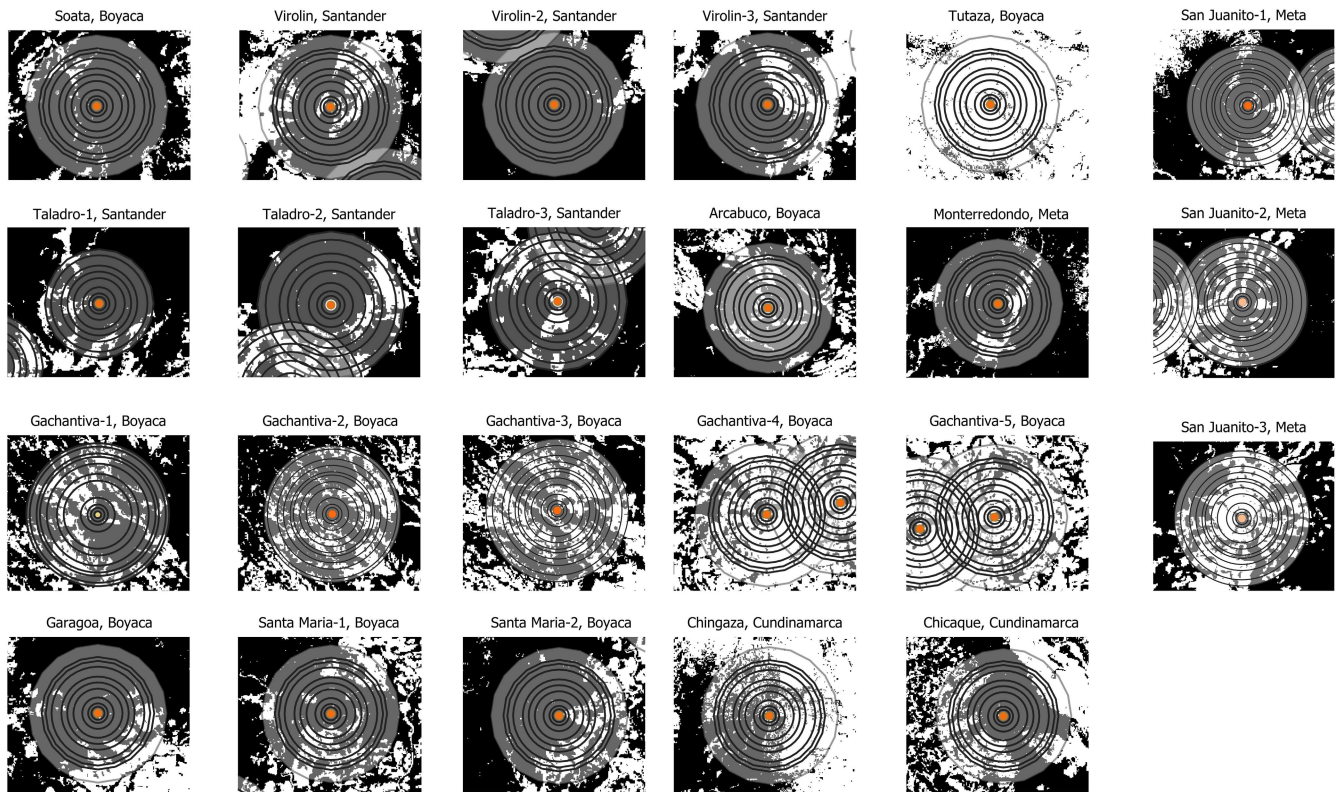
FIGURE 2 Location of studied forests ($n = 23$) along the eastern cordillera, Colombia. Maps depict forest cover (black), matrix (white), points represent (orange dots) the centroid of each forest, and buffers around each point represent the spatial extents analysed in our study (100–2400 m).

forest/non-forest map does not offer sufficient resolution to quantify scales below 100 m (30 × 30 m map resolution).

At each spatial extent, we quantified three landscape metrics linked to different ecological processes. First, habitat loss as the percent of forest cover (hereafter, forest cover) as a metric of habitat amount available in the landscape as a proxy of resource availability (Fahrig, 2013). Second, fragmentation as the number of forest patches present in the local landscape (also termed as fragmentation per se; Fahrig, 2013). The number of patches quantifies the process of habitat partitioning into small, unconnected fragments affecting landscape configuration (spatial arrangement of habitats). Third, edge density, calculated as the total length of forest edge divided by each spatial extent (associated with edge effects, Crouzeilles & Curran, 2016). Edge density quantifies the intensity of edge effects with higher values being characteristic of more fragmented forests. The premise was that the absence of forest leads to the depletion of hosts for epiphytic individuals. While other land covers, such as sparse trees in the pasture matrix and plantations, provide habitat for some epiphyte species, they have far lower species richness than later secondary or old-growth forests (Einzmann & Zotz, 2017; H. Einzmann & Zotz, 2016).

Landscape metrics were measured using the 30-m resolution "global change forest map" from 2018 (hereafter termed GCF; Hansen et al., 2013). We defined a threshold of 50% forest cover (non-forest <=50, and >50% as forest), after validating 334 field

points within and outside forest fragments to five forest cover thresholds (40%, 50%, 60%, 70%, 90%). To validate our threshold of 50% forest cover, we transformed all pixels into binary forest/non-forest maps for each threshold percentage, then we extracted the cover type of each of our 334 validation points, thus each point would be either forest or non-forest. Finally, we compared the proportion of points per threshold that matches our validation points and the threshold with the highest proportion of points was selected (Table S2). From this binary map, we calculated the proportion of forest cover in the landscape, number of patches of habitat (forest) and edge density exposed to the conditions of the non-forest habitat. We constrained our analyses to forest fragments with patch sizes >9 ha due to the resolution of GCF. Pixels were classified based on the nearest eight pixels connected in any direction allowing us to classify based upon the category of the majority of the surrounded pixels (McGarigal et al., 2012).

2.4 | Data analysis

We focused on two aspects of scale-of-effects: the direction and the spatial extent. We used a state-of-the-art modelling approach with linear mixed models (GLMM) with Poisson distribution errors to quantify the direction (positive, negative, or not significant correlation) and spatial extent of each landscape metric (forest

cover, fragmentation and edge density) on each response variable (species richness and total abundance) separately for orchids and NOE. Thus, each diversity metric at plot level was modelled independently with their own set of landscape metrics per spatial extent.

In each model, we included a nested spatial random effect (sampling points nested within forests) and an offset parameter (off-set=elevation) to account for the expected correlation between epiphyte species richness and elevation (Cardelus et al., 2006; Parra-Sanchez et al., 2023). All explanatory variables were standardized to have means equal to zero and two standard deviations to adjust for the differences in scales (z-transformation). We further explore a not significant effect of the predictors by using a null model, including only the intercept with the same structure of the models (i.e. error family, offset and response variable). Model assumptions were verified with marginal r-squared and residuals for each model were visually checked for normality and homoscedasticity (Nakagawa et al., 2017).

Although four spatial extents overlapped at 1500m extents (Figure 2), we found no spatial autocorrelations across these four models (Durbin-Watson-Test p: <0.05). Several studies have shown no evidence that overlapping landscapes compromised either spatial autocorrelation or the scale-of-effects (Zuckerberg et al., 2012, 2020). We, therefore, considered that our results are robust and conservative.

The direction of the scale-of-effects was obtained from each model (as the sign of each predictor's estimate) and illustrated by plotting the GLMM's estimates with confidence intervals (95%) to convey uncertainty. The spatial extent of the scale-of-effects was obtained as the difference between the model with the lowest Akaike-Information Criterion AIC value against the AIC of each individual model (ΔAIC) (Jackson & Fahrig, 2015). The range of spatial extents with ΔAIC <2 provide a comparable fit to the observed data. Thus, if all models fall into ΔAIC <2 or ΔAIC >2, there is not a detectable spatial extent. However, if, for example, a particular landscape metric from 100 to 1000m has an ΔAIC <2 but from 1000 to 1500m shows ΔAIC >2, then our spatial extent would be 100–1000m. We plotted the ΔAIC of each model as a dependent variable against its respective spatial extent to visually assess the spatial extent. Previous studies have used similar statistical approaches with Akaike's Information Criterion (Amiot et al., 2021; Gestich et al., 2019) and parameter estimates (Galán-Acedo et al., 2018), although the use of AIC has been criticized (Arnold, 2010; Galipaud et al., 2017).

Models considering fragmentation metrics and forest cover at the same time had multicollinearity issues >5 VIF (variation inflation factor) due to the high correlation among predictors (>0.80 in the fixed effects matrix correlation). The nature of this collinearity lies in the intrinsic link between habitat loss and fragmentation (Didham & Ewers, 2012; Fletcher et al., 2018; Püttker et al., 2020). Therefore, models with multiple predictors were excluded from the study.

2.5 | Software

All analyses were performed in R Statistical Software (R Core Team, 2021). Data manipulation was done with '*tidyverse*' (Wickham et al., 2019) and '*jtools*' (Long, 2019). Landscape metrics were computed with '*landscapemetrics*' (Hesselbarth et al., 2019), and generalized linear-mixed effect models were fitted using '*lme4*' and '*glmmTMB*' (Bates et al., 2015; Magnusson et al., 2017). Plotting was done using 'ggplot2' (Wickham & Winston, 2015) and 'sjPlot' (Lüdecke, 2023).

3 | RESULTS

3.1 | Epiphyte surveys

In total, we recorded 16,802 orchid individuals belonging to 332 species (273 species and 59 morphotypes), while 8782 individuals of NOE were found (non-orchids), with a range of 1 to 12 morphospecies in a single plot. Orchids were found in 88% of plots (n=125), while 96% of plots had NOE such as ferns (136 of 141 plots). We found the highest species richness in a forest plot with 28 species (bosque Andino, 18 orchids, 8 NOE) and 899 individuals (357 orchids, 542 NOE).

3.2 | Landscape context

Our results show that our forests have, in general, high levels of forest cover in the landscape. Considering the largest spatial extent (2400m), 69% of the sample forests had ~70% of forest cover (mean: 67%, range 5.9–100%), while between 61 and 78% of the sampled forests had a low number of patches (mean: 37.7, range 4–59), and low to middle levels of edge density (mean: 48.22 range: 10.64–77.62). Across sites, forest cover showed a consistent pattern of high cover at 100–200m (mean: 94.6%), decreasing as the spatial extent increases (mean: 72.2% at radii >800m; Figure S1). The number of patches constantly increased with spatial extent without reaching a plateau (Figure S1). Edge density was higher at the spatial extent between 100 and 800m, gradually flattening with the spatial extent (radii >800m; Figure S1).

3.3 | Spatial extent and impact of forest cover on community structure

The effect of forest cover on orchids and NOE was consistently positive across community-level metrics (species richness and total abundance), with the scale-of-effects detected at extents of 100–300m (GLMM forest cover, p<0.05, Figures 3 and 4; Tables S3 and S4). Likewise, the scale-of-effect of total abundance remains consistent at 200m (Figure S3; Tables S3 and S4), indicating that the significant relationship between forest cover and community-level metrics are

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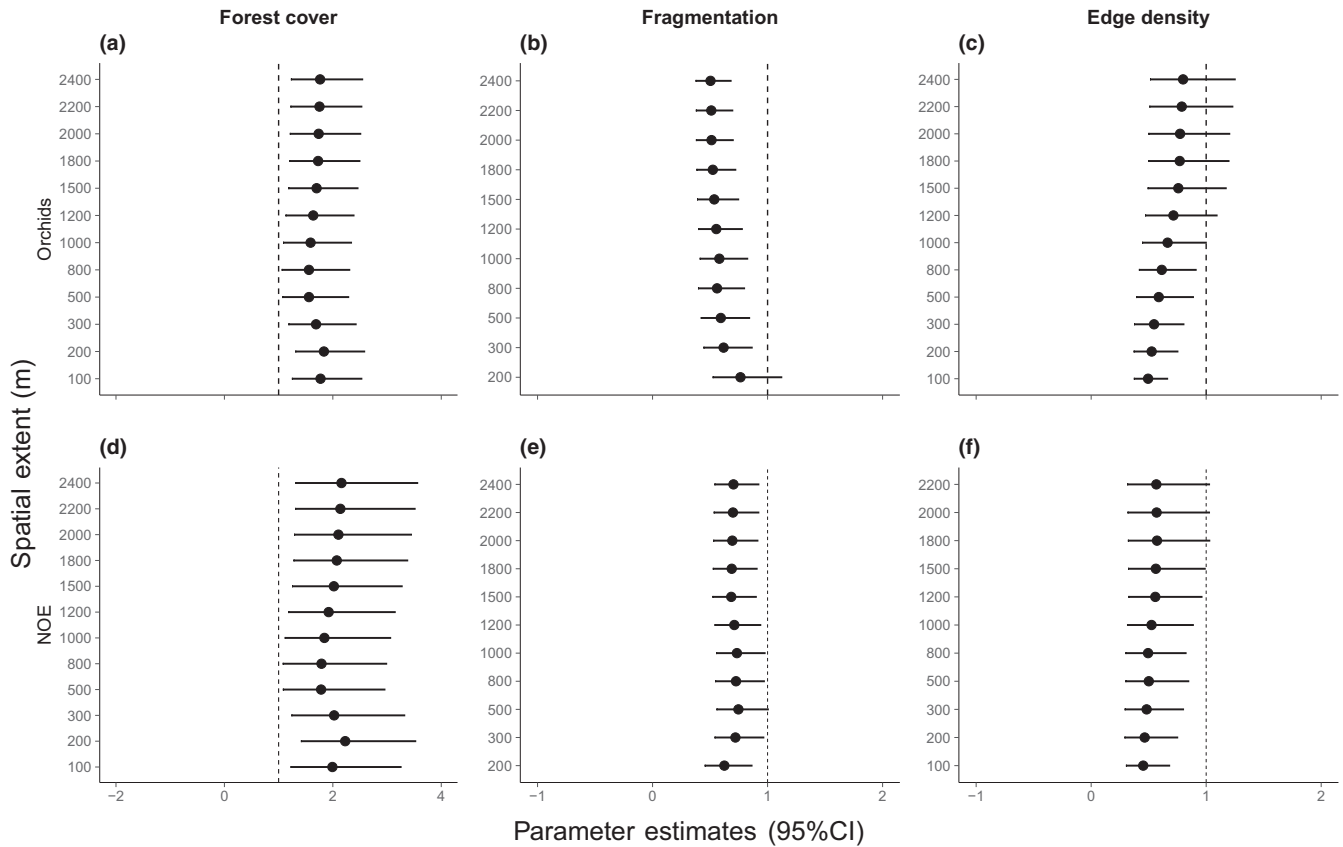
FIGURE 3 Direction of the effects of forest cover (%), fragmentation (number of patches) and edge density on orchids (a–c) and NOE communities (d–f) across 12 radii (100–2400 m) in the eastern cordillera of Colombia. Parameter estimates from generalized linear mixed effects models (GLMM) fitted to estimate the effects of each landscape predictor on species richness. Points indicate parameter estimates, error bars indicate 95% confidence intervals, and dashed lines show no effect.

detected at the same spatial scales. However, there was large uncertainty in confidence intervals and limited explanatory power of the models within the spatial extents of 500–1200 m across groups, but larger for orchids' total abundance (>300 m). This uncertainty suggests that the effect of forest cover might not be reliably detected within these spatial extents (Figure 3, Figure S4; Tables S3 and S4). The total explanatory power of the models is moderate (orchids' conditional pseudo-r^2=0.77–0.99; NOE' conditional pseudo-r^2=0.84–0.98) and marginal pseudo-r^2 ranges between 0.07 and 0.26 across metrics (Tables S3 and S4).

3.4 | Spatial extent and impact of fragmentation on community structure

Overall, the scale-of-effects of fragmentation is negative with species richness and total abundance, and detectable between 2000 and 2400 m on orchids and 200 m for NOEs (GLMM fragmentation, $p<0.05$; Tables S5 and S6). Fragmentation consistently exerts negative effects on orchid and NOE across spatial extents, but it is undetectable at 200 m in orchids and between 300 and 800 m in NOEs (models' performances were similar to null models, delta AIC=3.5–8.6; Figure 3; Tables S5 and S6). The explanatory power

of our models was moderate (orchids conditional pseudo-r^2=0.79–0.98; NOE conditional pseudo-r^2=0.54–0.74) and marginal pseudo-r^2 ranged between 0.04 and 0.32.

3.5 | Spatial extent and impact of edge effects on community structure

The edge density correlates negatively with our metrics and the scale-of-effects was detected between 100 and 200 m (Figure 3; Tables S7 and S8), but undetectable at spatial extents larger than 800 m (delta AIC=2.2–28.7; Figure 4). At extents ≥1000 m, models were not significant and showed ∆AIC close to the Null model (GLMM edge density, $p>0.05$; ∆AIC<5). In contrast, NOE' total abundance consistently showed a negative pattern with edge density and were significant across all spatial extents without affecting the scale-of-effects. The total explanatory powers of edge density models´ are moderate (NOE conditional pseudo-r^2=0.75–0.98; orchids conditional pseudo-r^2=0.82–0.98) and the component related to the fixed effects alone (marginal pseudo-r^2) ranged between 0.04 and 0.34.

Edge density was the landscape variable with the highest variance explained across models (Figures S2–S4; Tables S7 and S8).
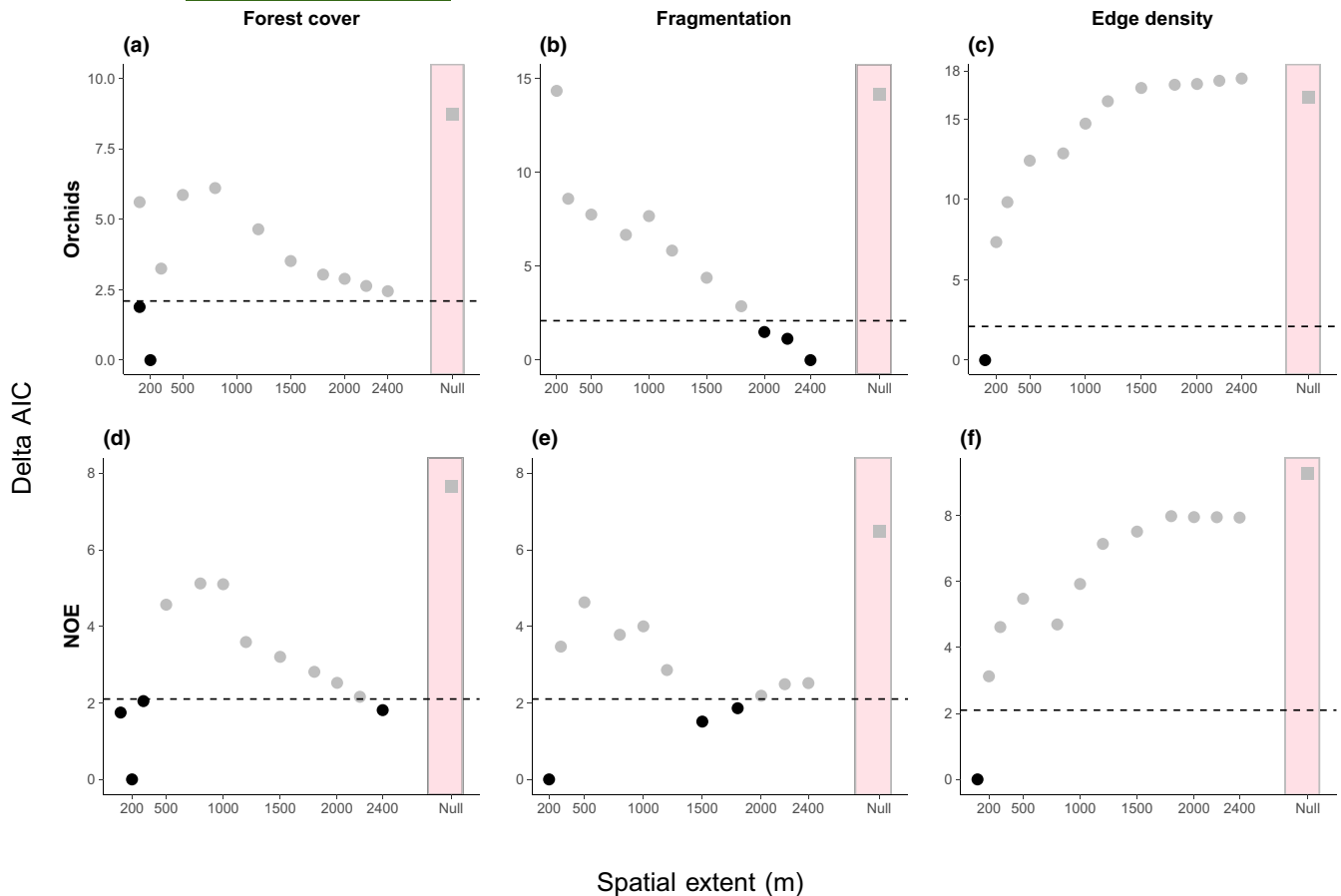
FIGURE 4 Scale of effect of forest cover (%), fragmentation (number of patches) and edge density orchids (a–c) and NOE communities (d–f) in the eastern cordillera of Colombia. Y-axis depicts the difference in Akaike's Information Criterion (Delta AIC) in linear mixed models of each landscape predictor on species richness ($q=0$). The null model includes only the intercept (pink shade). The dashed line represents the ΔAIC threshold (ΔAIC=2) were models have equivalent statistical support. Models with ΔAIC <2 are indicated with black symbols.

However, the null model was the least plausible model across response variables ($\Delta_i < 5$; Tables S3–S8). The scale-of-effects for forest cover, fragmentation and edge density overlapped at different spatial extents. This pattern demonstrates the connection between landscape processes and the scale at which they could interact (Figure 4; Figure S3).

4 | DISCUSSION

Unravelling the scale-of-effects (direction and spatial extent) at which landscape drivers shape biodiversity is key for theoretical and practical use. Our empirical study provides evidence that: (1) forest cover has positive effects on orchid and NOE communities across spatial extents, supporting our first expectation; (2) fragmentation and edge effects exert negative impacts on epiphyte diversity, supporting our second expectation, but these impacts are irrespective of the focal group and its scale dependence, rejecting our third expectation; and (3) choosing an inappropriate spatial extent might mask the effects of landscape processes on epiphytic communities. Preserving or improving forest cover, reducing edge effects at low

spatial extents (<500m radius) and reducing fragmentation at larger spatial extents (>2000m radius) are landscape strategies that might exert positive effects on epiphytic plant diversity.

4.1 | The effects of habitat loss and fragmentation on epiphytic communities

We found a consistent positive correlation between epiphytic communities and forest cover, especially between 100 and 200m (scale-of-effect), while the detectability was obscure across spatial extents <500 and >1200m. A high proportion of forest cover provides suitable conditions for a greater number of species to coexist and thrive (Arroyo-Rodríguez et al., 2020; Fahrig, 2013). We speculate this reflects sufficient availability of habitat in the landscape allowing species and individuals to reach suitable areas, while the opposite might occur in areas with lower forest cover (Ahuatzin et al., 2022; Arroyo-Rodríguez et al., 2020). However, the ecological processes and mechanisms involved in this response requires further study.

Fragmentation's effect on epiphyte communities is negative but its detection depends on the spatial extent. Fragmentation might

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affect understorey epiphytes by moderating large-scale processes at 2000–2400 m such as frequent dispersal due to lower connectivity across landscapes (Ewers & Didham, 2005). Furthermore, some reviews and empirical studies suggest that fragmentation is not important in landscapes with high forest cover in the landscape (e.g. >60%), because of the low variability in landscape configuration and high structural connectivity (Püttker et al., 2020; Villard & Metzger, 2014). Yet, fragmentation consistently impacts our understorey epiphytic communities in landscapes with high proportion of forest cover (69% of our landscapes have on average 70% of forest cover). Thus, the partitioning of the landscape might be enough to affect dispersal of Andean epiphytic communities (Mccormick & Jacquemyn, 2014; Mondragon et al., 2014). Further studies expanding the spatial extents might enhance our understanding on the effects of fragmentation on epiphytes (as the number of fragments increased constantly as the spatial extent increased; Figure S2).

We found that high edge density predicts lower species richness and abundance. We detected the scale-of-effects for total abundance of NOE (100–500 m), but not for orchids or NOE species richness (Jackson & Fahrig, 2015), which may suggest that epiphytic communities respond to edge effects below our spatial extents, as seen in other studies in the Colombian Andes (ca. 30 m, Parra-Sánchez et al., 2016). Epiphytic plants in the Brazilian Atlantic Forest show edge effects can penetrate at least 500 m inside forests and the abundance of 89% of epiphyte species in the canopy and understorey is negatively affected by edge effects reducing the conditions of the core area (Hernandez-Perez & Solano, 2015; Parra-Sanchez & Banks-Leite, 2020). Our results thus highlight the need to quantify edge effects and to create strategies to reduce their effects on biodiversity when designing or managing landscapes for conservation. This is especially important because much of the remaining tropical forest (>70%) globally is now near human-modified habitats (Haddad et al., 2015), pushing forest species to interact with edge conditions that might provide them with less optimal conditions (Ewers & Didham, 2005; Haddad et al., 2015; Tabarelli et al., 2012).

Our findings that fragmentation and edge effects negatively influenced both orchids and NOE might be counterintuitive for two reasons. First, most epiphyte species and all orchids have wind-dispersed propagules (Zotz, 2016), which should not restrict species dispersal (Einzmann et al., 2017). Second, our studied forests have a relatively high proportion of forest cover, which should decrease inter-patch isolation distances, favouring dispersal (Fahrig, 2013, 2017). Yet our results support the idea that epiphytes might be dispersal limited. Dispersal limitation is invoked in epiphytes because many species´ diaspores land very closely to their mother-plants (Acevedo et al., 2020; Cascante-Marín et al., 2009), and epiphyte communities present signalling of recruitment limitation and positive density dependence (Janzen et al., 2020) that might be involved in slow colonization events (Einzmann et al., 2021). Likewise, dispersal limitation might surge from tracking suitable conditions within forests due to the intrinsic dependency of some orchids to mycorrhizae colonies for germination that occur in clusters (McCormick

et al., 2018; Romero-Salazar et al., 2022). Hence, fragmentation and edge density might further exacerbate epiphytes' intrinsic dispersal limitation by increasing seed mortality of juveniles and seedlings due to dry conditions (Benzing, 1998; Migenis & Ackerman, 1993; Mondragón et al., 2015; Winkler et al., 2005), and forest-dependent species experiencing high mortality in human-modified habitats (Scheffknecht et al., 2010).

Detectability of the scale-of-effects depends on the spatial extent. Thus, landscape processes can be undetected if the spatial extent is chosen a priori or not explored at all. For instance, we found a consistent detrimental trend of habitat loss impacting both groups, but the high uncertainty in the estimates suggests that the effect of forest cover might not be reliably detected within 800–1200-m spatial extents (Figure 2). Low detectability may be a product of the interaction with other landscape drivers (edge density plateaus at 800 m) impacting the ability of epiphytes to disperse and utilize alternative habitats. Likewise, the role of fragmentation was undetected at extents of 200 m and edge effects at spatial extents >800 m. This might be a product of low landscape heterogeneity because fragmentation had the lowest values at 200 m (Figure S1), while edge density plateaus at extents >800 m. Thus, the observed pattern might be highly related to landscape variables and regional context, which suggests that landscape management strategies might provide positive impacts for both groups at the same spatial scale (Galán-Acedo et al., 2018; Smith et al., 2011).

The fact that scale-of-effects did not differ, in most cases, between orchids and NOE communities suggests that both groups are shaped by similar patterns and processes such as resource availability or community dynamics in the landscape (e.g. migrations, source-sink dynamics, adaptation to the same understorey microclimate; Ewers & Banks-Leite, 2013; Jackson & Fahrig, 2015; Smith et al., 2011). This might be the product of communities composed of highly ecologically equivalent species (Catchpole & Kirkpatrick, 2010). For instance, long-term monitoring of epiphytic communities has shown that short-distance dispersal and population growth are the dominant process shaping the community dynamics (Cascante-Marín et al., 2009; Einzmann et al., 2021; Einzmann & Zotz, 2017a, 2017b).

Preserving forest cover and reducing the impacts of fragmentation and edge effects have a direct and positive impact on epiphytes diversity at the adequate spatial extent. Hypothetically, if the direction of 'forest cover' is sustained across larger spatial extents than in our study, preserving epiphytes could be compatible with forest restoration strategies, in which the scale-of-effects of restoration actions is positive at buffers of 5–10 km (Crouzeilles & Curran, 2016). Indeed, epiphytes transplanted into forests under restoration had high survival rates in human-modified forests from radii <100 m (Reid et al., 2016).

4.2 | Conservation implications and conclusions

Our study suggests that preserving or increasing the amount of habitat at any spatial extent should promote epiphyte diversity,

although its positive impact might improve if combined with the reduction of fragmentation at coarse spatial (2000–2400 m) and edge effects at fine spatial (200 m) extents. The inclusion of strategies to reduce fragmentation and to maintain or increase forest cover at the same spatial extent would be positive for epiphytic diversity and a good starting point for designing biodiversity-rich landscapes in the tropics.

The constitution in Brazil and Colombia includes legislation to protect forests within private properties in rural areas. Private landowners are responsible for preserving at least 80% of native vegetation in the Brazilian Amazon, 30% in the Brazilian Cerrado and 20% in some Andean municipalities in Colombia (LEI No 12.651, de 25 de maio, 2012; Ley 388 de 1997, 1997). However, the landscape configuration of set-aside areas has not been regulated. Thus, the same percent of forest might be found in different small fragments or even fragmented corridors across private land, increasing edge effects. In terms of landscape management, including combined actions to preserve or encourage low fragmented landscapes with increasing forest cover at the same spatial extent (either at 100–300 m or 1500–2400 m) should have important benefits for conservation of these epiphytic plants. This scale is probably more suitable for bottom-up actions with stakeholders.

CONFLICT OF INTEREST STATEMENT
The authors have no relevant financial or non-financial interests to disclose.

DATA AVAILABILITY STATEMENT
The data sets generated during and/or analysed during the current study are available at figshare:10.6084/m9.figshare.22223893.v1.

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SUPPORTING INFORMATION

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