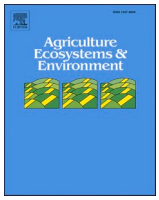
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When scale matters: Drivers of faunal diversity in cacao production landscapes in the Peruvian Amazon

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ABSTRACT

Preserving biodiversity in tropical agricultural areas relies on a fine balance between crop management strategies and landscape characteristics. Moreover, the response of different species to these local and landscape metrics may greatly differ. Therefore, identifying strategies to maximize biodiversity in tropical agricultural landscapes relies on analyses that encompass multiple spatial scales and taxa simultaneously. To address this, we assessed a multidiversity index, comprising the diversity of birds, bats, ground and flying insects in four different land uses in a highly deforested landscape in the Peruvian amazon basin: forest fragments, cacao monocultures, cacao agroforests and degraded areas, mainly covered by pastures and early successional vegetation. We identified the main biophysical drivers influencing annual multidiversity across the four land uses and across the dry and wet seasons. We complemented random forest (RF) analyses with generalized linear mixed-effects models. Our RF models explained between 46% and 62% of data variability, for annual multidiversity and for the dry and wet seasons. We observed that cacao growing in agroforestry systems held similar multidiversity values to those observed for forest fragments. Further, our findings provide specific management recommendations to integrate agricultural production with biodiversity conservation in a highly intervened landscape: such as the relevance of maintaining and increasing forest cover within the landscape as well as increasing the connectivity of tree-dominated land use types (i.e. agroforestry systems, forests fragments, agricultural areas mainly covered by trees).

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1. Introduction

Tropical countries hold the largest proportion of global forests (45%) and the highest global biodiversity, but at the same time concentrate ca. 90% of global deforestation rates that occurred between 1995 and 2025 (Bar-On et al., 2018; Song et al., 2018; Isbell et al., 2023; FAO, 2025). These alarming deforestation rates have increasing repercussions for biodiversity conservation, ecosystem stability, food security and the well-being of rural populations (Isbell et al., 2023). South America, in particular, has had the highest deforestation rates globally since 1990, despite an overall decline in recent years (FAO, 2025).

The largest share of deforestation in South America has been caused by agricultural conversion (Armenteras et al., 2017; Leblois et al., 2017; Curtis et al., 2018; Pendrill et al., 2022), resulting not only in habitat loss but also in increased fragmentation and habitat simplification, leading to terrestrial biodiversity loss (Pimm et al., 2014; Newbold et al., 2015; Curtis et al., 2018; Convention on Biological Diversity, 2020). Reconciling biodiversity conservation with productivity goals in tropical forest landscapes is therefore an increasingly recognized priority (Foley et al., 2005; Song et al., 2018; Bishop et al., 2025). To address this, two main strategies have emerged: retaining sufficient forest cover within the productive landscape matrix and integrating trees and other perennials in productive land uses, generally referred to as agroforestry (land sharing-sparing debate). For example, it has been reported that tropical species richness needs around 50% of minimum forest cover to be preserved. However, this threshold is not generally applicable and varies according to species needs, e.g. reaching up to 74% of forest cover for native birds (Shennan-Farpón et al., 2021). Not only the quantity but also the quality of forest cover in the landscape matters. Notably, the degree of forest fragmentation, the ecological connectivity between forest patches, as well as the structural diversity of forest vegetation have been found to influence the conservation of biodiversity in anthropogenic landscapes (Tscharntke et al., 2012; Haddad et al., 2015; Luther et al., 2020; Marjakangas et al., 2020; Martínez-Richart et al., 2025). Integrating these landscape configuration requirements into productive systems is an imperative need to bolster the conservation of wild biodiversity. In this context, agroforestry systems have the potential to complement the maintenance and connectedness of tree and forest cover within the landscape by creating structurally complex habitats in productive land uses that support higher species richness and functional diversity (in comparison to monocultures), delivering direct conservation benefits for plants, insects, birds, and soil microbes (Castle et al., 2022; Mathieu et al., 2025; Santos et al., 2019). Guiding the design of agricultural landscapes in the humid tropics that reconcile biodiversity conservation with productive activities thus requires reliable information on the recommended spatial scale and configuration of different land uses in the landscape matrix (Estrada-Carmona et al., 2022). Here we assess the role of different land uses and landscape characteristics in explaining the presence of multiple animal taxa in one of the main deforestation hotspots of the Peruvian Amazon in the Ucayali department.

We evaluated animal multidiversity — representing birds, bats, ground insects and flying insects— across four different land uses (i.e. fragments of secondary forest or degraded primary forest –hereafter forest fragments, cacao agroforests, cacao monocultures and degraded areas dominated by pastures), both across the wet and dry season in ten different locations for each land use. We characterized the vegetation, biophysical features, and both the local land-use and surrounding landscape characteristics of each of our sample sites. We used this information to assess which local plot- and landscape-level features most influenced multidiversity, and which animal taxa could be driving the observed patterns.

First, we hypothesized that carbon stocks in the soil at each sampling site would be a good predictor of multidiversity, as it has been found to covary with arthropod and vascular plant diversity in previous studies in South America (Peri et al., 2019; Flores-Ríos et al., 2020). Second, we hypothesized that multidiversity would differ among land uses, with forest fragments having the highest values, as the remnants of native habitats in the area (Wang et al., 2019), followed by cacao agroforestry. Finally, we hypothesized that landscape-level drivers would influence multidiversity more than local plot-level drivers, as landscape heterogeneity has been previously linked to higher diversity (Hackett et al., 2024).

2. Methods

2.1. Study area

Our study was developed in the Padre Abad province, located on the western part of the region of Ucayali, Peru, within the Amazon basin. The study area is part of the tropical rainforests and premontane rainforests of the Amazon basin, characterized by a predominantly warm and humid climate, with maximum temperatures reaching up to 31.9 °C in the dry season. Average rainfall in Ucayali reaches 2,344 mm with a peak during the wet season between February and May. The province of Padre Abad has experienced increased deforestation since 2002, resulting in the loss of ca. 73% of the original tree cover, most of which has been replaced by permanent agriculture (Global Forest Watch, 2025).

We selected ten farms from members of the organic cacao producers cooperative Colpa de Loros, and sampled different animal taxa within or nearby each farm in four distinct land-use types, for a total of 40 sample sites: (1) forest fragments, which the farmers declared not to deforest in the next years; (2) cacao agroforestry systems, including a variety of shade trees; (3) cacao monocultures, with only rare presence of other tree species, mostly along the edges; and (4) degraded lands, mostly covered by pastures and early successional fallows (Fig. 1). The selection of farms was guided primarily by the presence of cacao agroforestry systems of at least eight years old. This was the main limiting factor as agroforestry is relatively new in the region and at the time of research only twelve associated farmers of the cooperative Colpa de Loros complied. The ten resulting farms were selected from the twelve based on accessibility.

2.2. Farm and site data collection

At each sample site, we collected information about animal diversity, soil properties, as well as topographic and climatic variables. Animal diversity comprised assessments of avifauna, bats, flying insects, and ground insects at all sample sites. Biodiversity surveys were replicated in the dry season (August – October, 2022), and the wet season (April – June, 2023). Insect data was collected using malaise traps and pitfall traps. One malaise trap was located approximately in the center of each land-use patch, while nine pitfall traps were distributed in a 6 m × 6 m sampling grid, each trap separated by 3 m. All insects and arthropods collected were stored in 70% alcohol and identified at the Museo de Historia Natural, Universidad Nacional de San Marcos, in Lima, Peru. The order Lepidoptera was excluded from analyses because the preservation state of the collected specimens did not allow for reliable identification. We assessed bird diversity through point counts with a fixed radius of 35 m for ten minutes, discarding flyovers. We performed five rounds of point counts per sampling site in each season. We used mist-netting surveys to evaluate bat diversity using six nets (6 m x 12 m; 16 mm mesh size) per site. We performed two nights of surveys in each season, between 17:30 and 00:00, and each net was checked every 15 min. All captured bats were identified, measured and weighed before release.

To characterize soil properties, in August of 2023 we extracted three composite soil samples per site from the upper 30 cm layer of the soil. Each composite sample was composed of five subsamples. For each sample, we calculated the percentage of soil organic carbon (hereafter SOC) using the loss by ignition method, assuming a carbon concentra-

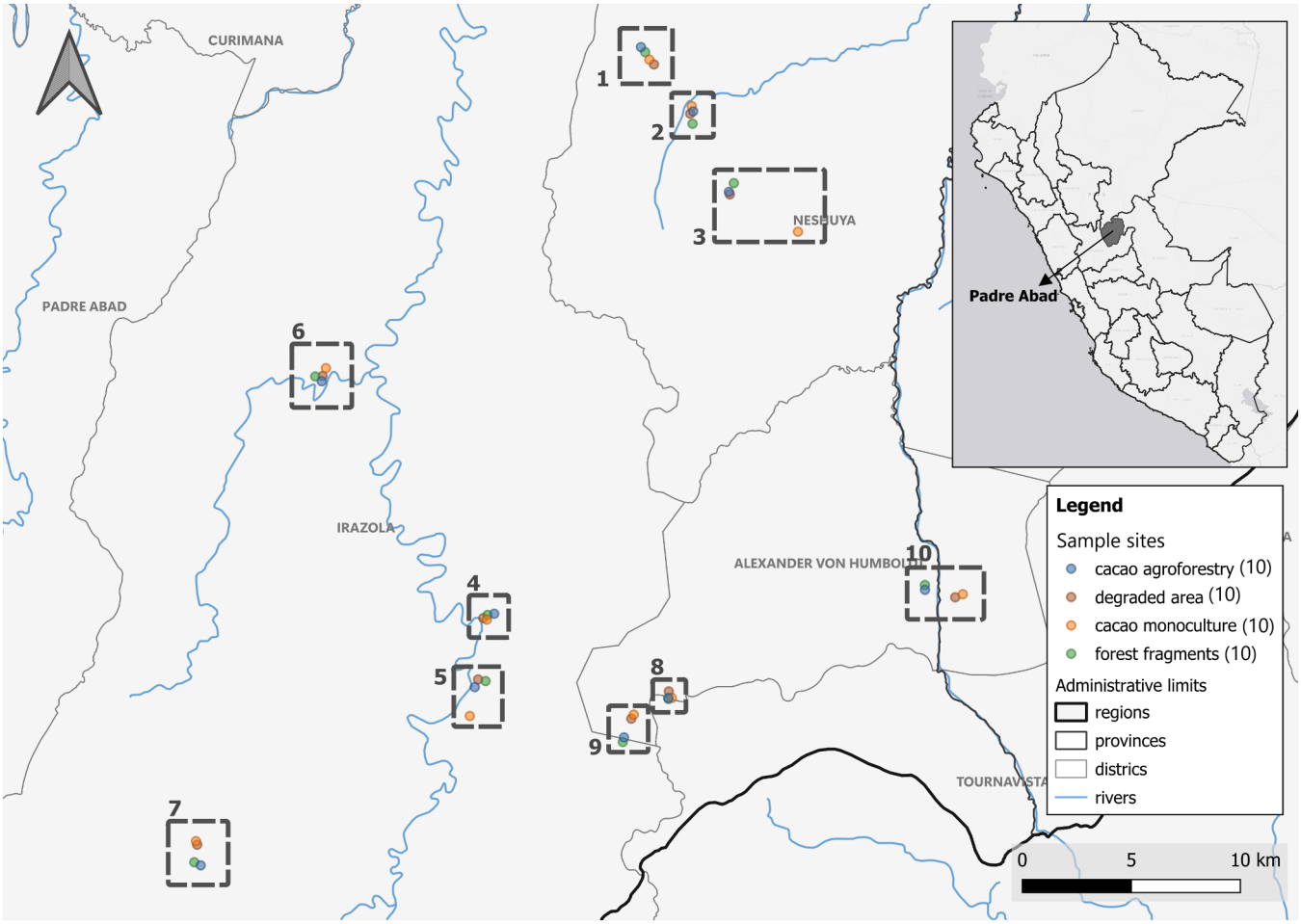


Fig. 1. Map of the 40 sample sites evaluated for the relevant drivers of multidiversity across different taxa in the region of Ucayali, Peru. The sites were categorized into four land-use types, indicated by colored dots: blue = agroforestry systems; green = forest fragments; red = degraded areas; yellow = cacao monocultures. Each set of four land uses were located in the close vicinity of 10 farms from organic cacao producers associated to the cooperative Colpa de Loros, as indicated by dashed rectangles.

tion of 58% (Nelson and Sommers, 1982; Guo and Gifford, 2002). Bulk density was estimated using a fixed volume cylinder and considering the sample weight after drying. We then calculated the SOC stock as (Eq. 1)

$$SOC = \%C * BD * z \quad \text{(Eq. 1)}$$

where %C is the carbon percentage, BD is the bulk soil density (g/cm^3) and z is the soil sampling depth (30 cm).

We complemented field information with georeferenced data. In this sense, topographic variables were extracted from 30 m spatial resolution Digital Elevation Models (DEMs), freely available from the shuttle radar topography mission (SRTM). We analyzed the DEMs in QGIS (version 3.38) and estimated the height above the nearest drainage (HAND), as an indicator of water table depth, accurately representing soil water environments (Nobre et al., 2011). Water table depth has emerged as a relevant driver of biodiversity, conditioning both floristic composition and faunal distribution (Francis et al., 2020; Gerolamo et al., 2022; Ferreira et al., 2023). We also measured the elevation, slope, and aspect for each sampling site from the SRTM DEM at 30 m spatial resolution.

3. Local and landscape characteristics

3.1. Biophysical and climate drivers

We extracted steepness information from the global landform classification map at 1 km spatial resolution. Here steepness is represented as the mean gradient slopes, representing specific physiographic regions (Iwahashi and Pike, 2007). We extracted soil order data from the SoilGrids taxonomy map at a 250 m spatial resolution (Hengl et al., 2017). Climatic drivers (mean annual temperature and annual precipitation) were derived from the WorldClim data at 1 km spatial resolution. The WorldClim dataset comprises historical climate data for ca. 40 years (Hijmans et al., 2005).

3.2. Patch size, proportional cover of the surrounding land uses and land-use cover diversity

We determined the patch size (ha) for each land-use unit that contained each of our sample sites (i.e. patch size of degraded land, cacao monoculture, cacao agroforestry and remnant forest area where sampling was carried out) and the distance from the sample site to the nearest edge of the land-use patch (m). We also measured characteristics of the landscape surrounding each sample site. To this end we used google satellite imagery available in QGIS for 2023, coinciding with the period of field sampling. We established buffers of 250 m, 500 m and 1000 m around each of our sampling sites to assess potential differences in the importance of landscape configuration variables at increasing spatial scales in explaining the animal diversity registered at our sampling sites. Within each buffer we categorized and manually digitalized all surrounding land uses into seven possible categories that could be identified via satellite imagery: (i) (sparse) agroforestry and regenerating vegetation, which includes open agroforests and vegetation under

natural regeneration; (ii) bareland, including all temporary openings with no vegetation mostly related to agricultural activities; (iii) built area, including all constructions, streets and roads; (iv) degraded areas or pasture; (v) monoculture (cacao and oil palm); (vi) water bodies, including all large rivers; and (vii) forests, which may also have comprised dense agroforests and degraded, previously harvested mature forests. Sparse agroforestry and natural regeneration were combined into one category because satellite images did not allow visually distinguishing between both (Aycart-Lazo et al., 2025). We then rasterized this manual classification at a 2 m spatial resolution. Based on the resulting layers, we determined within in each buffer size (i) the percentage cover of each of the 7 surrounding land use categories; and (ii) land use cover diversity, using the inverse Shannon index through the package *HillR* in R.

3.3. Connectivity and structure metrics

As part of the drivers describing the surrounding landscape, we also estimated connectivity and structure metrics using the same buffer sizes described previously. Habitat structure was characterized by using spaceborne LiDAR data from the Global Ecosystem Dynamics Investigation (GEDI) mission. GEDI uses a near-infrared laser to measure vertical vegetation profiles by exploiting the high reflectance of plant material in this portion of the spectrum, thereby capturing detailed canopy height metrics (Dubayah et al., 2020). We used GEDI L2A relative height (RH) metrics. The data was rigorously filtered to retain only high-quality footprints: quality flag $= 1$, degrade flag $= 0$, and sensitivity ≥ 0.95 (Dubayah et al., 2021; Beck et al., 2021). RH values exceeding 5 standard deviations from the mean were excluded as outliers. To create a continuous map from GEDI's discrete footprints, we spatially extrapolated RH metrics using Sentinel-1 radar and Sentinel-2 multispectral data. This approach follows established methods for modeling forest structure based on GEDI, integrating globally available satellite imagery (Potapov et al., 2021; Kacic et al., 2021). Predictor variables included annual median composites (2019–2023) of Sentinel-2 bands (blue, green, red, near-infrared (NIR), shortwave infrared 1 and 2 (SWIR-1, SWIR-2) and Sentinel-1 Radiometric Terrain-Corrected backscatter (VV, VH). A suite of vegetation indices was derived from these bands (see Appendix S1 for the full list). A vegetation mask, based on thresholds for the normalized difference moisture index (NDMI > 0.1), modified normalized difference water index (MNDWI ≤ 0) and Sentinel-1 VH backscatter (> -30 dB), was applied to exclude water and non-vegetated surfaces (Chen et al., 2020). Only masked pixels were used for model training and predictions; non-vegetated areas were assigned a value of 0. We focused on two key GEDI metrics: RH50 and RH95, representing the relative height at which 50% and 95% of the waveform energy is returned, corresponding to the median and near-top canopy heights, respectively.

To quantify local structural variability, we calculated the mean (μ) and standard deviation (σ) of RH50 and RH95 within a 100 m x 100 m (10 ×10 pixels) moving window. From these, we derived two integrative ratios: μRH50 / μRH95, the ratio of the median to top canopy height; σRH50 / σRH95, the ratio of their standard deviations. These ratios describe the vertical distribution and the horizontal heterogeneity of vegetation structure at the local scale.

To capture scale-dependent effects of habitat structure, all metrics were spatially aggregated by averaging their values within the buffers surrounding the sample sites at 250 m, 500 m and 1000 m. To quantify structural connectivity, a graph-theory framework was employed, which models the landscape as a network of habitat patches (nodes) connected by potential dispersal pathways (edges). This approach allows for the calculation of various connectivity metrics that characterize the potential for animal movement across the landscape (Pascual-Hortal and Saura, 2006). Habitat patches were determined using Enhanced Vegetation Index (EVI) (Eq. 2) given its improved performance over NDVI (Normalized Difference Vegetation Index) in high-biomass environments and reduced sensitivity to soil background and atmospheric interference (Liu and Huete, 1995; Huete et al., 2002). Patches of tree-dominated land uses were identified using Sentinel-2-based EVI thresholds between 0.5 and 0.8 (Huete et al., 2002; Faqe Ibrahim et al., 2023).

The resulting vegetation cover map had a 10 m spatial resolution and included two classes: tree dominated land uses (forest, agroforests and tree monocultures) and non-tree dominated land uses comprising agriculture (including bareland), built areas, or degraded areas.

$$EVI = 2.5 \times \frac{(NIR - RED)}{(NIR + 6 \times RED - 7 \times BLUE + 1} \quad \text{Eq. 2}$$

Habitat patches were treated as nodes in a graph, with connections established between patches whose borders were within a 25-meter threshold distance – reflecting the limited dispersal capacity and risk-averse behavior of understory birds (Bélisle and Desrochers, 2002). Connectivity metrics were computed using the *lconnect* package in R (Mestre and Silva, 2023) across the three spatial scales (250 m, 500 m and 1000 m). The following graph-derived metrics were computed: (i) number of components, representing the number of connected habitat patches with no connections to other groups within the landscape (ii) number of links, (iii) characteristic path length, (iv) surface of largest component, (v) mean size of components, (vi) integral connectivity index, (vii) edge density (see Appendix S1 for additional detail on the graph-derived metrics).

3.4. Data analysis

Following Allan, et al. (2014) we calculated a multidiversity index by scaling the site-level species richness values for each taxon (i.e. birds, bats, ground insects and flying insects), dividing them to the maximum observed value across all sample sites per season. We averaged the resulting scaled values across all taxa, considering a temporal approach: for each season separately (i.e. dry and wet), and for the whole year of sampling (i.e. annual approach). The multidiversity and specific taxa richness values were not significantly correlated, confirming that the multidiversity was not dominated by one or more animal taxa (Figure S1a, Appendix S1).

We then performed a three-step approach analysis to identify the main drivers of multidiversity. First, we used principal component analyses (PCA) to reduce model complexity by lowering the dimensionality of the potential drivers, considering that many of the landscape drivers measured at different spatial buffers showed high correlation (Figure S1b, Appendix S1). We performed eight PCAs across the drivers constructed for the three buffer sizes (250, 500 and 1000 m). These drivers were 1) land-use cover diversity, 2) forest cover, 3) agroforestry – regeneration cover, 4) bareland cover, 5) degraded areas cover and 6) monoculture cover (Figure S1c) and metrics related to 7) the connectivity of tree-dominated vegetation and 8) vertical vegetation structure. The metrics used for the two latter drivers corresponded to axes explaining $> 75\%$ of variability in data of PCAs constructed using all the different connectivity and vegetation structure parameters mentioned above. For each of the driver PCAs, we extracted the number of PCA axes needed to explain at least 75% of the variance in each category, which only in the case of land-use diversity, connectivity and structure were more than one axis. The first PCA axis of connectivity (connectivity C1) was mainly associated with the mean size of disjunct tree-dominated land use patches in the landscape and negatively with the number of disjunct patches. The second PCA axis (connectivity C2) was positively correlated with the total length of patch edges per unit area and path length between tree dominated patches (lower values mean higher connectivity, in this sense, the second axis represents an estimate of habitat fragmentation). The first PCA axis of vegetation structure (structure C1) was positively correlated with vegetation height and the density of the canopy and the second axis (structure C2) with higher vertical vegetation structure across the landscape. We checked the

resulting variables for connectivity and structure for multicolinearity through the use of variance inflation (VIF) calculations, with all retained variables yielding VIFs< 5. The selected axes from the PCA rounds were integrated into the second step analyses together with the drivers that were not estimated at different buffer sizes such as patch size, climate, soil and terrain variables.

In this second step, we ran three sets of random forests (RF) using multidiversity as response variable and considering the temporal dimensions of data, i.e. one for each season (wet and dry), and one for the annual multidiversity. We carried out 150 cross validations, creating 2000 trees each time. In each run, 80% of the data was randomly selected and used for model training and the remaining 20% for testing. The RF models were created using the *cforest* function in the *party* package for R (Hothorn et al., 2008). Relative importance of the drivers was calculated by using the *varimp* function. Complementary to the above RFs, we ran 12 additional RFs models (each with the same cross validation and settings as above): one for each of the different faunal diversity data we collected (birds, bats, flying insects and ground insects), and replicated for each season (dry and wet) and for the annual dataset (4 x 3 = 12). The analyses for insects were split into trap type (i.e. malaise and pitfall) due to the methodological differences for each trap. We also computed partial dependence (PD) curves for the top 6 drivers identified in each of the RFs models to visualize their average marginal effects on multidiversity. The PD were estimated via the *GetPartialData* function in the *moreparty* package in R (Friedman, 2001; Goldstein et al., 2015).

In a third step, we used the results of the RF analyses to select the five variables with highest influence on multidiversity values in each season and across the whole year. We used these to construct generalized linear mixed effect models in the *glmmTMB* package (Magnusson et al., 2020) for three main reasons. First, to assess the relevance of interactions between land use and other selected drivers. Second, to validate the direction and significance of the effects of the selected variable on our multidiversity metrics uncovered by the PD curves. And third, to evaluate potential differences in the importance of landscape configuration variables at increasing spatial scales (250, 5000 and 1000 m) in explaining observed multidiversity. Therefore, in this step, we included the drivers measured at different buffer sizes instead of using the PCA axes obtained from the first step. All models included the site identity as a random effect, to account for potential spatial correlation between the four land-uses in each farm and were run using either a gaussian or Gamma distribution, according to residual fit, which we tested using the *DHARMa* package (Hartig, 2024). We performed model selection using the *MuMIn* package (Bartoń 2023). We dredged all models and selected the best models as those with lowest AICc values. In cases in which model selection resulted in more than one best model (lowest AICc values with $\Delta AICc < 2$), we report significance values for the model with the lowest AICc, and a summary of the presence of each predictor in the full set of best models (see Appendix S2).

When one of the predictors selected by the RF models was a variable assessed at different spatial scales (e.g. forest cover or degraded cover at 250 m, 500 m and 1000 m around the sample sites), we ran different models for each of the three spatial scales. We selected the best model among the three scales using AICc comparison and an ANOVA test. If the models did not differ significantly in their predictive quality, we performed model selection for all spatial scales and reported best models for the three scales. Otherwise, we selected the best model among the three scales and performed model selection as described previously only for this model.

4. Results

We recorded 182 bird species, 54 bat species (i.e. ~10% and ~30% of all bird and bat species, respectively, currently known to occur in Peru, Medina et al., 2023; Pacheco et al., 2021; Plenge and Angulo, 2026), 861 insect morphospecies in pitfall traps and 614 morphospecies of insects in Malaise traps. We observed higher mean annual multidiversity values in those sample sites located in forest fragments (0.651 ± 0.160), followed by cacao agroforestry systems (0.565 ± 0.119), degraded areas (0.514 ± 0.063) and cacao monocultures (0.431 ± 0.078). When comparing the multidiversity values across climatic seasons, we observed that while forest fragments held the highest multidiversity values in the dry season (0.512 ± 0.128), in the wet season there was no reported statistical difference between multidiversity across the sample sites (Fig. 2a,b,c, see Table S1 in Appendix S1 for detailed summary). All animal taxa, except bats, showed highest richness values at sample sites during the dry season and there was large species turnover between dry and wet season (Fig. 2d).

4.1. Effects of local and landscape drivers on multidiversity

The models obtained from the RF analyses explained between 46% and 62% of the variability in multidiversity (Figure S3, Appendix S1). The main drivers influencing multidiversity identified by the RF analyses differed between the climatic seasons and annual measurement. Annual multidiversity was most influenced by the patch size of the land use containing the sample sites, the land-use type, the percentage of forest cover in the surrouning landscape, the level of connectivity of tree dominated land-use types and the percentage of monoculture cover (Fig. 3). The top drivers of multidiversity in the dry season were similar to those identified for annual multidiversity, with patch size of the land use sampled; land-use type; connectivity of tree dominated land-use types (connectivity C1); percentage of forest cover; and habitat structure, explained by the variance in canopy height of tree dominated land uses within the landscape (structure C1) being the top 5 variables (Fig. 3). Similarly, the most influential drivers of multidiversity during the wet season were the patch size of the sampled land use, followed by the level of fragmentation of tree dominated land uses in the landscape (connectivity C2),;water table depth (i.e. HAND); terrain steepness and the mean size of connected tree-dominated land uses (connectivity C1) (Fig. 3). Table 1 provides an overview of the general trends between the explanatory variables and multidiversity for the six most important variables, based on PD curves presented in Appendix S1.

Our GLMM models showed higher annual multidiversity with increasing percentage of forest cover in a 250 m radius in forest fragments, but no other land-use category showed a significant relationship with forest cover. In the wet season, the percentage of degraded land cover (250 m) was negatively associated with multidiversity in agroforestry and forest fragments (Fig. 4, Table S2 in Appendix S2). We did not observe any relevant interactions between land use and other drivers for the dry season.

Similarly to the RF results, our regressions showed significant differences in multidiversity among the four land uses in both the dry and wet season, as well as across the whole year. Other significant drivers during the dry season were the mean size of connected tree-dominated land uses surrounding the sampling site, inverse of number of unconnected components in the landscape (connectivity C1) and patch size of the sampled land use. Finally, the depth of the water table also influenced multidiversity in the wet season (Fig. 4, Table S2 in Appendix S2).

4.2. Effects of local and landscape characteristics on single taxa groups

The RF for different faunal diversity data were able to explain between 51% and 60% of bat richness data variability (Figure S4 in Appendix S1), between 53% and 58% of bird richness data variability (Figure S5 in Appendix S1), between 56% and 74% of insect richness data variability collected via pitfall traps (i.e. ground insects, Figure S6 in Appendix S1) and between 50% and 56% of insects richness data variability collected via malaise traps (i.e. flying insects, Figure S7 in Appendix S1).

The top drivers for annual bat richness were related to elevation, patch size of the sampled land use, annual mean temperature, height

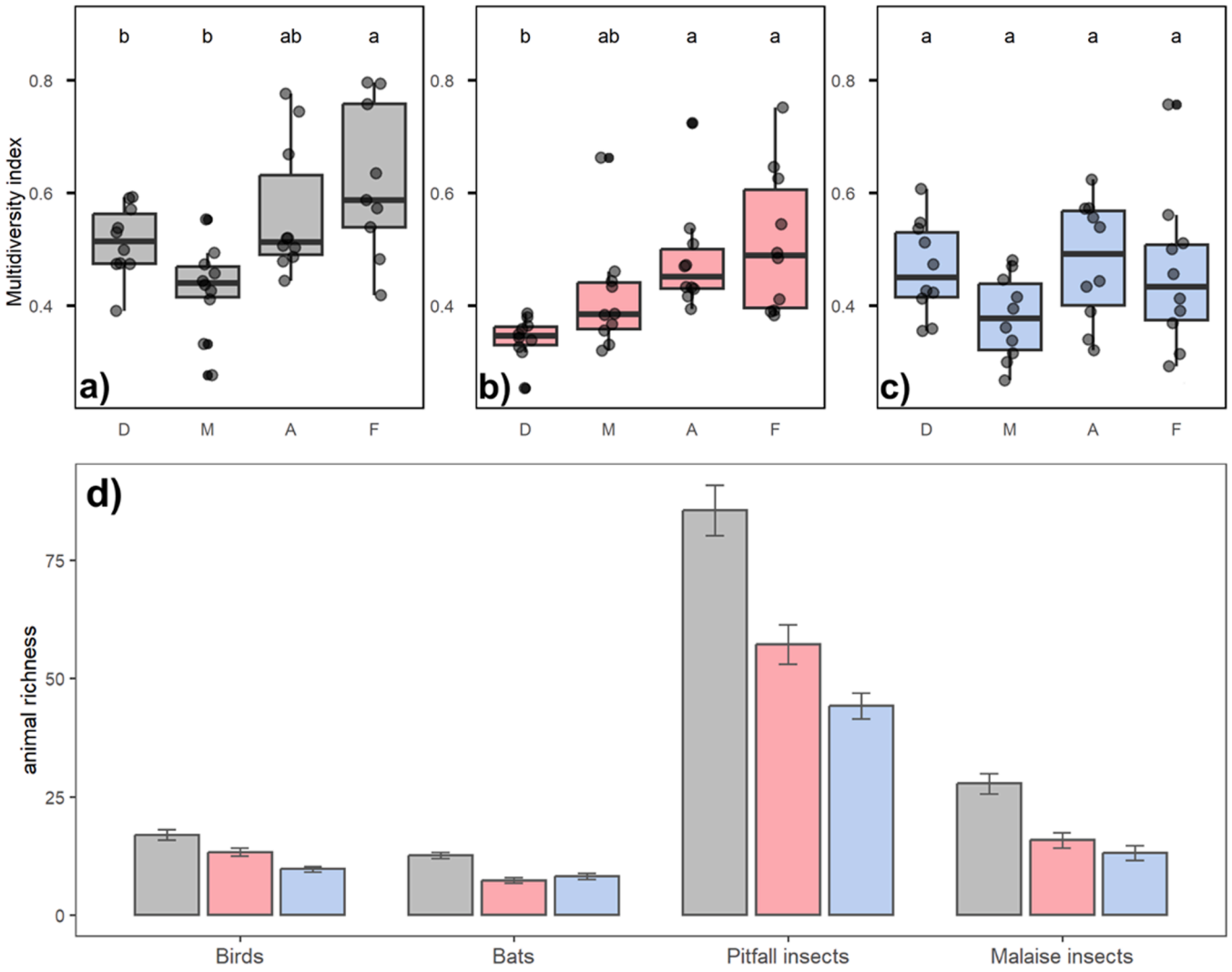


Fig. 2. Observed a) annual multidiversity and across the b) dry and c) wet seasons. Boxplots represent medians and interquartile ranges, points indicate individual observations, and different letters mean statistically significant differences among land-use categories based on Tukey post hoc tests after ANOVA. F= forest fragments, A= cacao agroforestry, M= cacao monoculture, D= degraded land. Panel d) shows the mean ± SE richness values per animal group. For all boxplots, gray represents annual values, light red, the dry season and light blue, the wet season.

variability of tree-dominated vegetation within the landscape (structure C2), water table depth and the level of fragmentation of tree-dominated land uses in the landscape (connectivity C2) (Table 1). Similarly, dry-season bat richness was mainly driven by patch size, followed by annual precipitation and elevation; whilst top drivers for wet-season richness were mainly related to height variability of tree-dominated vegetation within the landscape (structure C2), the level of fragmentation of tree dominated land uses in the landscape (connectivity C2), and land use. Top drivers for annual bird richness were related to terrain slope, the percentage of monoculture cover and habitat fragmentation (connectivity C2). Bird richness during the dry season was driven by the percentage of monoculture cover, patch size of the sampled land use and the land-use type, while wet season richness was driven by habitat fragmentation (connectivity C2), terrain slope and the height and/or density of canopies of tree-dominated vegetation in the landscape (structure C1) (Table 1, Appendix S1).

The top drivers for insect richness collected via pitfall traps were similar across our temporal assessments, and were mainly related to percentage of forest cover, land-use type, patch size of the sampled land use and habitat fragmentation (connectivity C2). Top drivers of annual insect richness collected via malaise traps, were land-use type, the percentage of forest cover and connectivity among tree dominated land use types (connectivity C1). The top drivers for dry-season insect richness were mainly related to height and/or density of canopies of tree-dominated vegetation in the landscape (structure C1), land-use diversity and land-use type. Finally, top drivers for wet-season insect richness were steepness, the percentage of forest cover and land-use diversity (Table 1, Appendix S1).

5. Discussion

Our results show that the size of continuous land-use patches, land-use type, the cover of forest fragments and the connectivity of tree-dominated land uses in the landscape, stood out as the most important drivers of multidiversity across the year. This confirms our hypothesis that biophysical predictors associated with the landscape are more relevant for defining multidiversity in transformed habitats than local site conditions alone, although local conditions such as land-use also influenced multidiversity values. Against our expectations, SOC stocks did not affect multidiversity. As expected, forests fragments held the highest multidiversity values followed by the sample sites located in agroforestry systems, particularly during the dry season probably due to resources being scarcer in the other land uses. These results suggest that not only the production of crops in agroforestry systems, but also the size

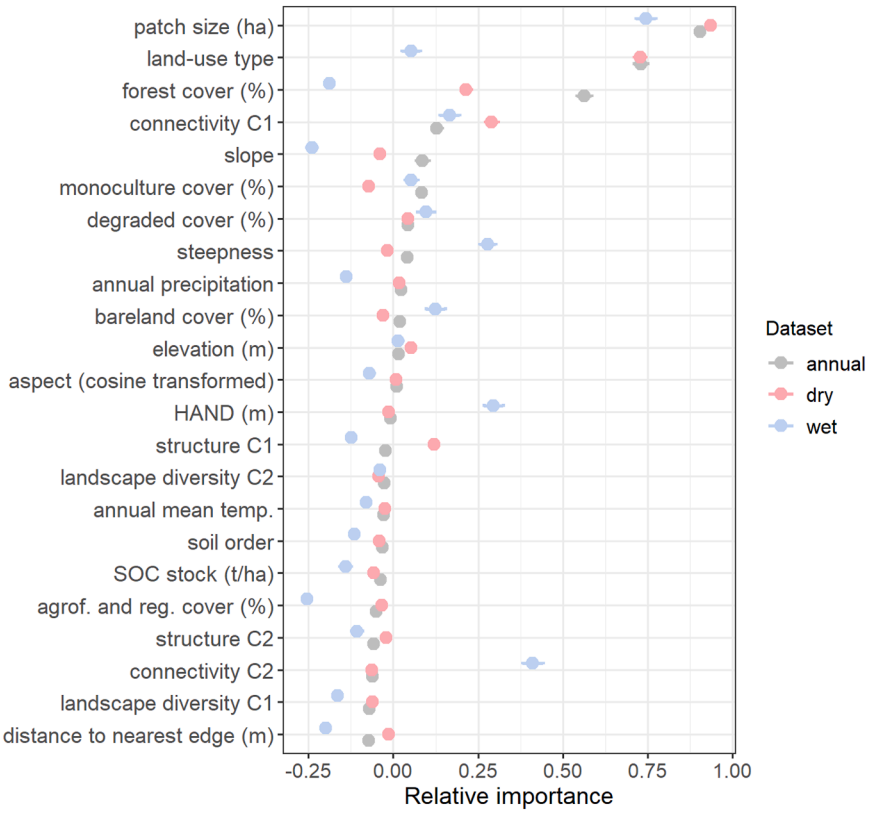


Fig. 3. Relative importance values for the drivers included in the Random Forest models for annual, dry and wet seasons' multidiversity.

Table 1
Overview of the general directions of the relations between the top 6 explanatory variables of faunal diversity based on the RF models and the derived PD curves. "+" indicates a positive effect of explanatory variables on faunal diversity evaluated across the whole year (Ann) and across the dry and wet seasons; "-" indicates a negative effect, "∩" indicates a unimodel correlation. For land-use type the land uses yielding highest diversity values are listed. Land use types: F= forest fragments, A= cacao agroforestry, M= cacao monoculture, D= degraded land. Empty cells mean that those variables were not among the top 6 variables according to the computed relative variable importance derived from the RF models. See Appendix S1 for detailed information on the connectivity and structure metrics.

Drivers	**Mutidiversity**			**Bat**			**Bird**			**Pitfall insects**			**Malaise insects**		
	Ann	**Dry**	**Wet**	**Ann**	**Dry**	**Wet**	**Ann**	**Dry**	**Wet**	**Ann**	**Dry**	**Wet**	**Ann**	**Dry**	**Wet**
land-use type	**F&A**	**F&A**				**A&M**	**D+F+A**	**F**	**D**	**F**	**F**	**F**	**F&D**	**F**	**D&F**
forest cover	+	+								+	+	+	+		+
degraded cover		-	-									-	-		
monoculture cover	-						-	-				-			
land use diversity at 500 and 1000 m buffer size														+	-
patch size	+	+	+	+	+		+	+		+	+	+			
distance to nearest edge									-	+					
connectivity C1 - mean size of connected tree dominated land uses, inverse of number of unconnected components in the landscape	+	+	+										+	+	
connectivity C2 - level of fragmentation of tree dominated land uses in the landscape			+	+		+	+		+	-	-	-			-
vegetation structure C1 -height and/or density of canopies of vegetation in the landscape		+							-				+	+	
vegetation structure C2 – canopy height variation of vegetaion in the landscape				+		+		+		-	-				-
elevation				-	-	-		-							
steepness	+		+		+										+
depth water table			-	-	-	-	-		-						
slope							-		-					-	
aspect								-					∩		
mean temperature				+	+	+									
annual precipitation					-						-			+	

of a continuous patch and the maintenance of forests and connectivity of tree-dominated land-use types in the wider landscape are essential for maintaining tropical biodiversity in highly deforested agricultural landscapes, especially when climatic conditions make resources scarce.

During the wet season, when resources are more abundant across the landscape (coinciding with peak net primary productivity and nutrient

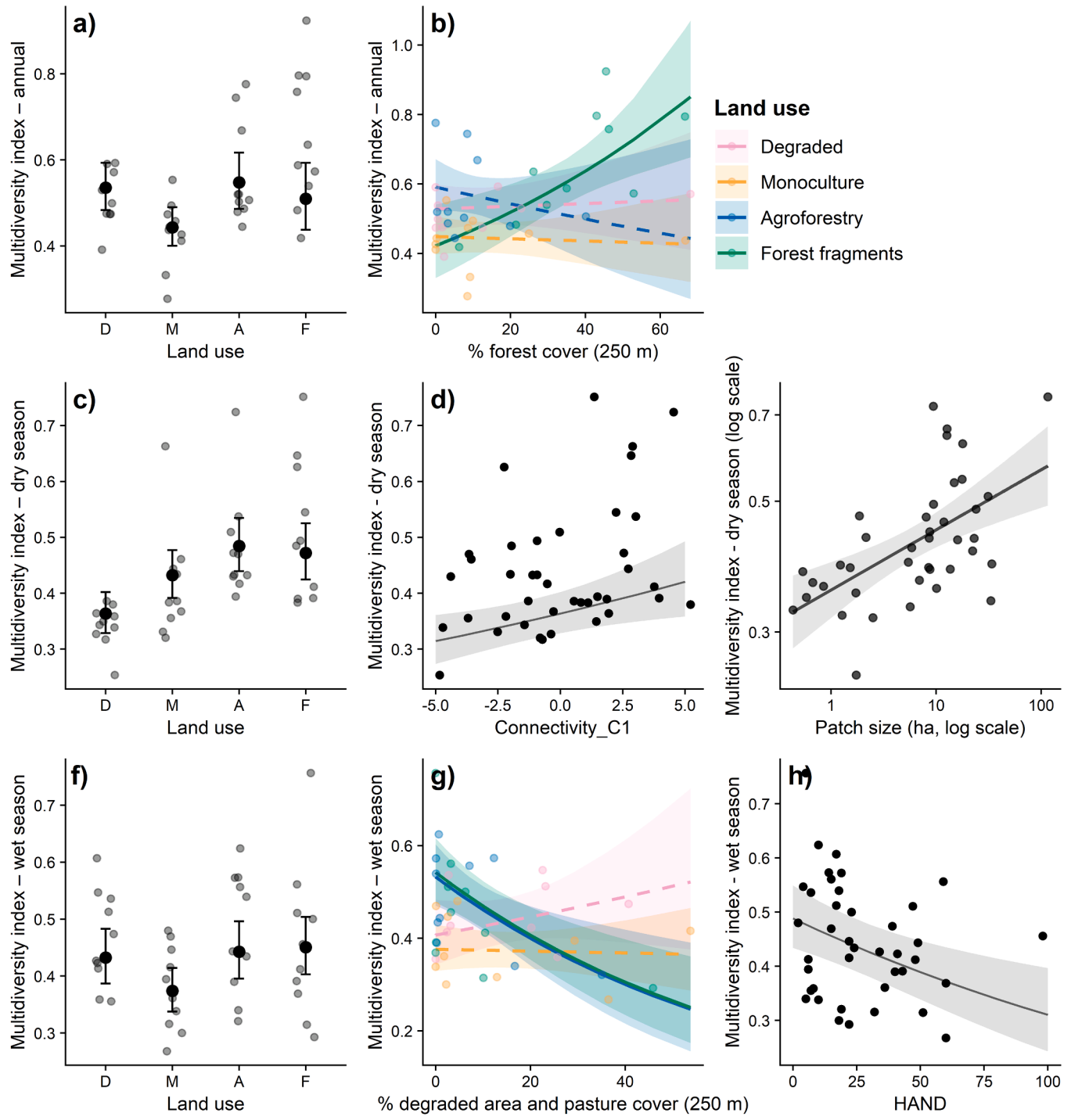


Fig. 4. Effects of the drivers obtained from the best GLMM models and annual multidiversity (a,b), dry-season (c,d,e) and wet-season (f,g,h) (see Appendix S2 for further information about the models). For models representing interactions (b) and (g): solid lines represent significant interactions, dashed lines, non-significant interactions. Lines represent GLMM predictions, and shaded bands indicate 95% confidence intervals. Land-use types of the sampled sites: F= forest fragments, A= cacao agroforestry, M= cacao monoculture, D= degraded land. HAND= height above nearest drainage, as an estimator of water table depth. For further detail see Table S2 in Appendix S2.

cycling; Xu et al., 2015; Manu et al., 2024) multidiversity was more evenly distributed across land uses. This could be attributed to complementary habitat effects that exist in transformed landscapes, where distinct land-use patches provide complementary niches that sustain higher beta species richness (Knoke et al., 2016; Hackett et al., 2024). The main trends in multidiversity were not predominantly driven by any of the single animal groups we sampled, which often responded in opposite directions to landscape and site-level variables (Appendix S1). Hence, divergent site conditions, landscape and plot-level management interventions may differently influence the presence and diversity of specific animal groups.

1. Crop production in agroforestry systems can host similar multidiversity levels as forest fragments within heterogeneous landscapes

Multidiversity was reported to be highest in forest fragments and agroforestry, especially during the dry season, this pattern was also

observed for the whole year (annual multidiversity). This is consistent with agroforestry systems functioning as supplementary foraging habitats when resources become scarce in the dry season, likely reflecting the effects of the structural complexity of agroforestry systems relative to monoculture or open areas, which favors overall animal species richness and endemic multidiversity (Wurz et al., 2022; Rajaonarimalala et al., 2024). Other animal groups reached higher values in other land uses. For example, bird and flying insect communities in degraded areas showed higher richness particularly in the wet but not the dry season, likely because of intermediate disturbances that allow the temporary presence of species with different degrees of habitat specialization (Connell, 1978). Therefore, having a dynamic vegetation matrix might have positive overall effect, supporting the existence of different taxa (Hackett et al., 2024) by containing a larger diversity of temporal and spatial niches in comparison to more homogeneous landscapes (Bazzaz, 1975; Tilman, 1982; Chesson, 2000). An ample body of evidence exists showing that landscape heterogeneity (both compositional and configurational) allows for the development of complementary resources and inter-field connectivity, because it incorporates different habitat types into the landscape matrix allowing for different species communities to thrive (Tscharntke et al., 2012; Hekkala et al., 2023; Montoya-Sánchez et al., 2023; Priyadarshana et al., 2024).

However, even within a heterogeneous matrix, certain landscape characteristics interact with the capacity of specific land uses to host higher levels of multidiversity. Notably, the cover of degraded areas in the landscape surrounding our sample sites had a negative effect on the multidiversity found in agroforests and forest fragments but not in monocultures . This emphasizes that, within land-use diversity, vegetation simplification and loss is still a limitation for biodiversity (Tscharntke et al., 2012).

2. Higher forest cover in the surrounding landscape enhances animal diversity

The amount of forest cover in the landscape positively influenced the animal multidiversity recorded at our sampling sites, and particularly of insects collected in both malaise and pitfall traps. This finding is aligned with previous observations on the relevance of forest cover on animal richness (Millard et al., 2021; Achury et al., 2025). For example, moths tend to be more diverse and abundant in forests in comparison to grasslands, given the higher resource availability and heterogeneity in the former compared to the latter (Achury et al., 2025). Similarly, the diversity of tropical pollinators has been found to decrease in areas with more intense land uses, even in comparison to non-tropical environments (Millard et al., 2021). Retaining key ecosystem services associated to flying insects, such as crop pollination, therefore depends on retaining and restoring forest cover around productive land uses.

The fact that bird and bat diversity were less influenced by the forest cover in the landscape may be because bird and bat functional diversity is known to closely follow processes of habit disturbance and loss, as well as processes of forest recovery (Falconí-López et al., 2024). As such, long-standing deforestation processes in the study region may have resulted in an overall low presence of forest specialists. Aycart-Lazo et al. (2025) found similar results in the neighboring department of San Martin and argued that the level of forest cover in the wider landscape serves a filter in selecting specific functional groups of birds that are more likely to forage and establish in different land uses within the landscape, including cacao agroforests (Aycart-Lazo et al., 2025). Low landscape level forest cover might as such have already filtered out forest specialists, which would only be able to recolonize the landscape after a long process of active or passive forest restoration efforts (Metz et al., 2023). However, this pattern could also be confounded by increased vocal activity and detectability during the breeding season, which we cannot fully disentangle with the current dataset.

The fact that the amount of forest cover in the landscape was not an important variable in explaining multidiversity during the wet season is probably due to the more even availability of food resources across all land uses when rainfalls promote higher vegetation and arthropod biomasses mentioned above (Manu et al., 2024).

3. The patch size of a given land use positively enhances the multidiversity it can host

The bigger the land use patch, the fewer edge effects and more stable habitat conditions, allowing for higher multidiversity values. Especially in the tropics, communities living near the edge tend to be less diverse in comparison to those living far from it (Willmer et al., 2022). Patch size has also been found to influence α-diversity of Lepidoptera and Orthoptera in temperate climates (Perrin et al., 2025). In the tropics, the level of insect specialization will drive the response of a certain species towards habitat loss. For example, closed-canopy specialists and species that feed on dead wood, such as termites, show overall declines in abundance and diversity as a result of habitat reduction (Hamer et al., 2003; Hilker et al., 2014; Stork et al., 2017; Thorn et al., 2018). In our study, this effect was also driven by bats, pitfall insects and birds. But birds also reported higher diversity closer to the margins of the land-use patches we sampled. The high diversity of birds in ecotones or transitional habitats such as forest edges is well known (e.g. Nguyen et al., 2025) and is associated to the diversity of resources (including vegetation from different ecosystems), which may attract species adapted to both open areas and densely vegetated forests. However, these ecotones tend to be temporary foraging habitats for most bird species, which may make use of them, but still require other well-conserved and structurally complex habitats to persist.

4. Ecological connectivity in the landscape enhances animal diversity

The two dimensions of ecological connectivity identified from the RF analyses had variable effects on animal diversity. Landscapes with larger (and hence fewer) disjunct tree-dominated land use patches had positive effects on multidiversity, and particularly flying insects throughout the year and during the dry season. Larger tree-dominated land use patches might host higher diversity of these animal groups for the more stable habitat conditions and resources they offer compared to smaller patches, particularly during the dry season (Ferreira et al., 2017). Further, higher fragmentation of tree-dominated land uses in the landscape (expressed as higher edge density and larger path lenghts) had a positive influence only on wet-season multidiversity and the richness of birds and bats during annual and wet season, respectively, but had a negative influence on insects collected with both pitfall and malaise trap. This could reflect that insects are less tolerant to habitat fragmentation, while the resident (non forest- specialist) bird and bat populations might be able to take advantage of a more fragmented vegetation more effectively during the wet season possibly due to landscape complementation (Dunning et al., 1992). These findings align with the expectation of ecological theory that connectivity can increase biodiversity by improving movement possibilities for different taxa across the landscape, and in general increasing the availability of suitable habitats, depending on their mobility (Fahrig, 2003; Fahrig et al., 2011), especially in highly deforested landscapes, as the one in our study area (Cunningham et al., 2025).

Similar to our above argument that most forest-specialist bird and bat species may have disappeared from the study region, also the high level of fragmentation of vegetation in the landscape may have filtered out low mobility species. Notably, in the case of bats, habitat fragmentation and forest loss results most of all in the disappearance of low-mobility and large animalivorous species (Farneda et al., 2015), which contribute essential ecosystem services for agricultural areas, including cacao plantations, such as pest control (Vansynghel et al., 2022a; Ocampo-Ariza et al., 2023). Therefore, guaranteeing ecological connectivity, even through tree lines or live hedges interconnecting tree-dominated land uses is pivotal to restore and retain key ecosystem service provision in tropical agricultural landscapes. This is also key for promoting flying insect diversity (Vansynghel et al., 2022b).

5. Structure complexity of vegetation in the landscape has distinct effects on animal diversity

The mean height of vegetation in the landscape surrounding our sampling sites positively influenced the diversity of flying insects and

negatively influenced bird diversity during the wet season. In forest areas such as the amazon basin, vegetation height is well correlated with forest age (Vlam et al., 2017), and consequently the availability and stability of resources and microclimatic conditions which may impact the diversity of low-mobility animals such as insects. Further, vegetation with the tallest and denser canopy in the landscape is of course forest followed by agroforests, suggesting that landscapes with higher mean vegetation size host higher forest cover which promotes flying insect diversity as discussed above. It also aligns with our hypothesis that bird species that are forest specialists may have become less abundant in the study region as a consequence of the high deforestation rates, and hence the negative relation of the remaining species with higher canopies found in relict forest.

On the other hand, increasing vegetation heights may increase the presence of cryptic species which are difficult to detect (Morelli et al., 2022) and may have been disproportionately missed during our point counts.

While bat and bird diversity benefited from a more complex vegetation structure in terms of tree height (higher height variation) within the landscape, the opposite effect was found for insects, which were negatively influenced by a more complex structure. This is in line with previous studies in temperate forests, which found that height heterogeneity negatively affected the diversity of several arthropod groups, while bats did not respond significantly to this variable (Heidrich et al., 2023). Neotropical bats are considerably more diverse in morphology and flight preferences than temperate ones and may therefore benefit more from complex height structure, in which small bats with different foraging and flying traits thrive simultaneously, guaranteeing niche complementarity (Farneda et al., 2015). This high functional diversity of bats may be detrimental for flying insects, which may experience increased predation pressure from bats.

In contrast to bats, local soil arthropods communities are known to specialize according to land-use type (Crotty et al., 2023). Considering that higher vegetation vertical structure in the broader landscapes implies a higher turnover between different land uses, this might prevent arthropod communities to reach highest levels of diversity as opposed to landscapes with larger patches of the same land use (preferably forest) and hence lower vertical vegetation variation. A similar explanation might to some extent apply to flying insects whose diversity was negatively influenced by land use diversity in the wider landscape, at least in the wet season.

6. Site specific abiotic variables

In spite of the limited geographical range covered by our study sites topographic and hydrologic variables contributed to explaining the variation in multidiversity we found.

The relevance of terrain steepness for higher diversity of flying insects and bats could be related to the availability of different niches in the landscape (Stein et al., 2014). In our study, steepness classification represents physiographic regions rather than local slope grandients. Therefore, in the amazon context, even a slight rise in the terrain in comparison to the surroundings can be considered as steep (relative to the surrounding level terrains, Iwahashi and Pike, 2007) representing landscape topography variations rather than local steepness.

More shallow water tables positively influenced the diversity of bats and birds. This finding may reflect the influence of water table depth on biomass productivity, as deeper water tables likely limit water accessibility for vegetation growth, which could limit vegetation height and structure complexity (Ehbrecht et al., 2021; Sousa et al., 2022). The negative relationship between annual precipitation and insects collected with pitfall traps may be explained by their overall lower diversity during the wet season (Fig. 2). Thus, increased annual precipitation during the dry season could create environmental conditions resembling those of the wet season, leading to similar reductions in diversity. By contrast, higher water availability during the dry season may promote increased breeding rates of flying insects – collected with malaise traps (van Dijk et al., 2024).

Future studies should incorporate broader environmental gradients -particularly greater variation in topography and water availability- to better assess how local and landscape-level abiotic factors interact to shape the diversity of different taxa groups. In addition, integrating functional group classifications would provide a more mechanistic understanding of how distinct ecological roles respond to landscape configuration in human-dominated environments.

6. Conclusions

We evaluated the relationship between multidiversity—comprising the richness of multiple animal groups (birds, bats and insects, collected via malaise and pitfall traps)—and both local- and landscape-level drivers across four land-use types in a human-dominated region of the Peruvian Amazon. Tropical seasonality (dry vs. wet seasons) influenced multidiversity patterns among land uses, underscoring the importance of resource availability, particularly during the dry season. Cacao agroforestry systems supported multidiversity levels most similar to those of forest fragments. Overall, landscape metrics exerted a stronger influence on multidiversity than local drivers. Multidiversity increased with larger patch sizes, higher forest cover in the surrounding landscape, and greater connectivity among tree-dominated vegetation.

These findings provide clear guidance for biodiversity-oriented management strategies in productive and highly modified tropical landscapes. They emphasize the need to move beyond plot-level management and consider broader landscape structure, recognizing that conservation outcomes depend not only on the focal land use but also on the surrounding habitat mosaic.

Although our models captured consistent multidiversity patterns, substantial unexplained variation remained, reflecting the complexity of ecological systems. Model performance could be further improved by incorporating functional group classifications to better capture differential ecological responses. Future research should also integrate finer temporal resolution, additional environmental drivers, and functional diversity metrics to refine our understanding of these relationships.

CRediT authorship contribution statement

Sandra Duarte-Guardia: Writing – review & editing, Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Carolina Ocampo-Ariza:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **Isaura Menezes:** Writing – original draft, Visualization, Formal analysis, Data curation. **Fernando Cerna:** Writing – review & editing, Investigation. **Jorge E. Carrera:** Writing – review & editing, Methodology, Investigation. **Mauricio Ugarte:** Writing – review & editing, Methodology, Investigation. **Yohamir Casanca:** Writing – review & editing, Methodology, Investigation. **Luis Figueroa:** Writing – review & editing, Investigation, Data curation. **Mabel Alvarado:** Writing – review & editing, Investigation, Data curation. **Fernando Paz:** Writing – review & editing, Investigation. **Hendel Mateo:** Writing – review & editing, Investigation. **Mateo Nicoli:** Writing – review & editing, Investigation. **Carlos Poppe:** Writing – review & editing, Investigation. **Juniors Molina:** Writing – review & editing, Investigation. **Camila Cuya:** Writing – review & editing, Investigation. **Jean Luc Martin:** Writing – review & editing, Investigation. **Susan Medina:** Writing – review & editing, Investigation. **Brenton Ladd:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Evert Thomas:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT 4.1 to optimize and improve coding when analyzing the data. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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.

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Authors contribution

E.T, S.D, C.O.A, B.L conceptualized the study, S.D, C.O., I.M. and E.T. curated the dataset, ran the analyses and drafted the manuscript.

I.M., S.D., C.O. and C.C. worked in the GIS derived data related to the classification of land-use types, percentage of land-use covers and connectivity and habitat structure metrics.

S.D., M.N., C.P., J.M., C.C. and J.L.M. collected the insects data in wet and dry seasons.

S.M., M.A., L.F., H.M., M.N., C.P., J.M., C.C. and J.L.M. participated in the classification and identification of insects and arthropods.

M.U. and Y.C. participated in the identification and characterization of birds for the wet and dry seasons.

F.C., J.C. and J.M. participated in the identification and characterization of bats for the wet and dry seasons.

S.D. and J.M., collected the soil samples.

All authors contributed to the revision and editing of the manuscript.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110760.

Data availability

The data supporting the findings of this study is publicly avaiable at: 10.5281/zenodo.22878248

References

Beck, J., Wirt, B., Armston, J., Hofton, M., Luthcke, S., and Tang, H., 2021, Global Ecosystem Dynamics Investigation (GEDI) level 2 user guide, 25 p.
Achury, R., Staab, M., Seibold, S., et al., 2025. Habitat and land-use intensity shape moth community structure across temperate forest and grassland. J. Anim. Ecol. 94. https://doi.org/10.1111/1365-2656.70132.
Allan, E., Bossdorf, O., Dormann, C.F., et al., 2014. Interannual variation in land-use intensity enhances grassland multidiversity. Proc. Natl. Acad. Sci. USA 111, 308–313. https://doi.org/10.1073/pnas.1312213111.
Armenteras, D., Espelta, J.M., Rodríguez, N., Retana, J., 2017. Deforestation dynamics and drivers in different forest types in Latin America: three decades of studies (1980–2010). Glob. Environ. Change 46. https://doi.org/10.1016/j.gloenvcha.2017.09.002.
Aycart-Lazo, P., Ivañez-Ballesteros, B., Ocampo-Ariza, C., et al., 2025. Landscape context influences local management effects on birds and bats in Amazonian cacao agroforestry systems. Agric. Ecosyst. Environ. 385. https://doi.org/10.1016/j.agee.2025.109545.
Bar-On, Y.M., Phillips, R., Milo, R., 2018. The biomass distribution on Earth. Proc. Natl. Acad. Sci. USA 115. https://doi.org/10.1073/pnas.1711842115.
Bartoń K. (2023) MuMIn: Multi-Model Inference; R Package Version 1.47.5; R Foundation for Statistical Computing: R package ver 1475.
Bazzaz, F.A., 1975. Plant species diversity in old-field successional ecosystems in southern Illinois. Ecology 56. https://doi.org/10.2307/1934981.
Bélisle, M., Desrochers, A., 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. Landsc. Ecol. 17. https://doi.org/10.1023/A:1020260326889.
Bishop, G.A., Kleijn, D., Albrecht, M., et al., 2025. Critical habitat thresholds for effective pollinator conservation in agricultural landscapes. Science 389, 1979. https://doi.org/10.1126/science.adr2146.
Castle, S.E., Miller, D.C., Merten, N., et al., 2022. Evidence for the impacts of agroforestry on ecosystem services and human well-being in high-income countries: a systematic map. Environ. Evid. 11. https://doi.org/10.1186/s13750-022-00260-4.
Chen, X., Liu, L., Zhang, X., et al., 2020. A novel water change tracking algorithm for dynamic mapping of inland water using time-series remote sensing imagery. IEEE J. Sel. Top. Appl. Earth Obs. Remote. Sens. 13, 1661–1674. https://doi.org/10.1109/JSTARS.2020.2983729.
Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31. https://doi.org/10.1146/annurev.ecolsys.31.1.343.
Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1979. https://doi.org/10.1126/science.199.4335.1302.
Convention on Biological Diversity2020. Perspectiva Mundial sobre la Diversidad Biológica 5.
Crotty, F.V., Demirer, U.A., Norris, S.L., et al., 2023. Evaluating the impact of long-term land use change and age since disturbance on soil faunal diversity. Forests 14. https://doi.org/10.3390/f14091882.
Cunningham, C.A., Beale, C.M., Bowler, D.E., et al., 2025. Connectivity benefits most woodland invertebrate species but only in landscapes with low woodland cover. Ecol. Lett. 28.
Curtis, P.G., Slay, C.M., Harris, N.L., et al., 2018. Classifying drivers of global forest loss. Science 361, 1979. https://doi.org/10.1126/science.aau3445.
Dubayah, R., Blair, J.B., Goetz, S., et al., 2020. The global ecosystem dynamics investigation: high-resolution laser ranging of the earth's forests and topography. Sci. Remote. Sens. 1. https://doi.org/10.1016/j.srs.2020.100002.
Dubayah, R., Hofton, M., Blair, J., Armston, J., Tang, H., & Luthcke, S. (2021). GEDI L2A Elevation and Height Metrics Data Global Footprint Level V002 [Dataset]. NASA Land Processes Distributed Active Archive Center. https://doi.org/10.5067/GEDI/GEDI02_A.002.
Dunning, J.B., Danielson, B.J., Pulliam, H.R., 1992. Ecological processes that affect populations in complex landscapes. Oikos 65, 169–175.
Ehbrecht, M., Seidel, D., Annighöfer, P., et al., 2021. Global patterns and climatic controls of forest structural complexity. Nat. Commun. 12. https://doi.org/10.1038/s41467-020-20767-z.
Estrada-Carmona, N., Sánchez, A.C., Remans, R., Jones, S.K., 2022. Complex agricultural landscapes host more biodiversity than simple ones: a global meta-analysis. Proc. Natl. Acad. Sci. USA 119. https://doi.org/10.1073/pnas.2203385119.
Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34.
Fahrig, L., Baudry, J., Brotons, L., et al., 2011. Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol. Lett. 14, 101–112. https://doi.org/10.1111/j.1461-0248.2010.01559.x.
Falconí-López, A., Mitesser, O., Martin Schaefer, H., et al., 2024. Habitat niches of bird species along a recovery gradient in the Chocó tropical forest. Ecol. Indic. 166. https://doi.org/10.1016/j.ecolind.2024.112260.
FAO2025. Global forest resources assessment 2025. FAO.
Faqe Ibrahim, G.R., Rasul, A., Abdullah, H., 2023. Sentinel-2 accurately estimated wheat yield in a semi-arid region compared with Landsat 8. Int. J. Remote. Sens. 44. https://doi.org/10.1080/01431161.2023.2232542.

Farneda, F.Z., Rocha, R., López-Baucells, A., et al., 2015. Trait-related responses to habitat fragmentation in Amazonian bats. J. Appl. Ecol. 52. https://doi.org/10.1111/1365-2664.12490.
Ferreira, D.F., Rocha, R., López-Baucells, A., et al., 2017. Season-modulated responses of Neotropical bats to forest fragmentation. Ecol. Evol. 7. https://doi.org/10.1002/ece3.3005.
Ferreira, M.M., Xavier, B., da, S., Bobrowiec, P.E.D., et al., 2023. Bat diversity is driven by elevation and distance to the nearest watercourse in a *terra firme* forest in the northeastern Brazilian Amazon. J. Trop. Ecol. 39, e1. https://doi.org/10.1017/S0266467422000438.
Flores-Ríos, A., Thomas, E., Peri, P., et al., 2020. Co- benefits of soil carbon protection for invertebrate conservation. Biol. Conserv. https://doi.org/10.1016/j.biocon.2020.108859.
Foley, J.A., DeFries, R., Asner, G.P., et al., 2005. Global consequences of land use. Science 309 (1979), 570–574.
Francis, E.J., Asner, G.P., Mach, K.J., Field, C.B., 2020. Landscape scale variation in the hydrologic niche of California coast redwood. Ecography 43, 1305–1315. https://doi.org/10.1111/ecog.05080.
Friedman, J.H., 2001. Greedy function approximation: a gradient boosting machine. Ann. Stat. 29. https://doi.org/10.1214/aos/1013203451.
Gerolamo, C.S., Costa, F.R.C., Zuntini, A.R., et al., 2022. Hydro-edaphic gradient and phylogenetic history explain the landscape distribution of a highly diverse clade of lianas in the Brazilian Amazon. Front. For. Glob. Change 5. https://doi.org/10.3389/ffgc.2022.809904.
Global Forest Watch2025. Global forest watch: a resource for monitoring forest change and climate change. In: globalforestwatch.org.
Goldstein, A., Kapelner, A., Bleich, J., Pitkin, E., 2015. Peeking inside the black box: visualizing statistical learning with plots of individual conditional expectation. J. Comput. Graph. Stat. 24. https://doi.org/10.1080/10618600.2014.907095.
Guo, L.B., Gifford, R.M., 2002. Soil carbon stocks and land use change: a meta analysis. Glob. Chang. Biol. 8, 345–360. https://doi.org/10.1046/j.1354-1013.2002.00486.x.
Hackett, T.D., Sauve, A.M.C., Maia, K.P., et al., 2024. Multi-habitat landscapes are more diverse and stable with improved function. Nature 633. https://doi.org/10.1038/s41586-024-07825-y.
Haddad, N.M., Brudvig, L.A., Clobert, J., et al., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1. https://doi.org/10.1126/sciadv.1500052.
Hamer, K.C., Hill, J.K., Benedick, S., et al., 2003. Ecology of butterflies in natural and selectively logged forests of northern Borneo: the importance of habitat heterogeneity. J. Appl. Ecol. 40. https://doi.org/10.1046/j.1365-2664.2003.00783.x.
Hartig F.2024. DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version 047.
Heidrich, L., Brandl, R., Ammer, C., et al., 2023. Effects of heterogeneity on the ecological diversity and redundancy of forest fauna. Basic. Appl. Ecol. 73. https://doi.org/10.1016/j.baae.2023.10.005.
Hekkala, A.M., Jönsson, M., Kärvemo, S., et al., 2023. Habitat heterogeneity is a good predictor of boreal forest biodiversity. Ecol. Indic. 148. https://doi.org/10.1016/j.ecolind.2023.110069.
Hengl T., Jesus J.M.De, Heuvelink G.B.M., et al2017. SoilGrids250m: global gridded soil information based on machine learning.
Hijmans, R.J., Cameron, S.E., Parra, J.L., et al., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978. https://doi.org/10.1002/joc.1276.
Hilker, T., Lyapustin, A.I., Tucker, C.J., et al., 2014. Vegetation dynamics and rainfall sensitivity of the Amazon. Proc. Natl. Acad. Sci. USA 111. https://doi.org/10.1073/pnas.1404870111.
Hothorn T., Hornik K., Strobl C., Zeileis A.2008. party: A Laboratory for Recursive Part (y)itioning: R package. v 1.3-1. R package version 09-0, URL http://CRAN R-project org.
Huete, A., Didan, K., Miura, T., et al., 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. Remote. Sens. Environ. 83. https://doi.org/10.1016/S0034-4257(02)00096-2.
Isbell, F., Balvanera, P., Mori, A.S., et al., 2023. Expert perspectives on global biodiversity loss and its drivers and impacts on people. Front. Ecol. Environ. 21. https://doi.org/10.1002/fee.2536.
Iwahashi, J., Pike, R.J., 2007. Automated classifications of topography from DEMs by an unsupervised nested-means algorithm and a three-part geometric signature. Geomorphology 86, 409–440. https://doi.org/10.1016/j.geomorph.2006.09.012.
Kacic, P., Hirner, A., Da Ponte, E., 2021. Fusing Sentinel-1 and -2 to Model GEDI-Derived Vegetation Structure Characteristics in GEE for the Paraguayan Chaco. Remote Sens. 13 (24), 5105. https://doi.org/10.3390/rs13245105.
Knoke, T., Paul, C., Hildebrandt, P., et al., 2016. Compositional diversity of rehabilitated tropical lands supports multiple ecosystem services and buffers uncertainties. Nat. Commun. 7. https://doi.org/10.1038/ncomms11877.
Leblois, A., Damette, O., Wolfersberger, J., 2017. What has driven deforestation in developing countries since the 2000s? Evidence from new remote-sensing data. World Dev. 92. https://doi.org/10.1016/j.worlddev.2016.11.012.
Liu, H.Q., Huete, A., 1995. Feedback based modification of the NDVI to minimize canopy background and atmospheric noise. IEEE Trans. Geosci. Remote. Sens. 33. https://doi.org/10.1109/36.377946.
Luther, D.A., Cooper, W.J., Wolfe, J.D., et al., 2020. Tropical forest fragmentation and isolation: Is community decay a random process? Glob. Ecol. Conserv. 23. https://doi.org/10.1016/j.gecco.2020.e01168.
Magnusson A., Skaug H., Nielsen A., et al2020. Package "glmmTMB." R package version 1.0.2.1.
Manu, R., Iddris, N.A.A., Corre, M.D., et al., 2024. Response of tropical forest productivity to seasonal drought mediated by potassium and phosphorus availability. Nat. Geosci. 17, 524–531. https://doi.org/10.1038/s41561-024-01448-8.
Marjakangas, E.L., Abrego, N., Grøtan, V., et al., 2020. Fragmented tropical forests lose mutualistic plant–animal interactions. Divers. Distrib. 26. https://doi.org/10.1111/ddi.13010.
Martínez-Richart, A.I., Zolles, A., Oettel, J., et al., 2025. A review of structural and functional connectivity studies in European forests. Landsc. Ecol. 40.
Mathieu, A., Martin-Guay, M.O., Rivest, D., 2025. Enhancement of agroecosystem multifunctionality by agroforestry: a global quantitative summary. Glob. Chang. Biol. 31. https://doi.org/10.1111/gcb.70234.
Medina, C.E., Medina, Y.K., Pino, K., et al., 2023. New records of bats from Peru. Rev. Peru. Biol. 30. https://doi.org/10.15381/rpb.v30i2.24867.
Mestre, F., Silva, B., 2023. lconnect R package: a versatile tool for evaluating landscape connectivity and prioritizing habitat patches in conservation research. Ecol. Modell. 484. https://doi.org/10.1016/j.ecolmodel.2023.110489.
Metz, T., Blüthgen, N., Drossel, B., 2023. Shifts from non-obligate generalists to obligate specialists in simulations of mutualistic network assembly. Oikos 2023 (7), e09697. https://doi.org/10.1111/oik.09697.
Millard, J., Outhwaite, C.L., Kinnersley, R., et al., 2021. Global effects of land-use intensity on local pollinator biodiversity. Nat. Commun. 12. https://doi.org/10.1038/s41467-021-23228-3.
Montoya-Sánchez, V., Kreft, H., Arimond, I., et al., 2023. Landscape heterogeneity and soil biota are central to multi-taxa diversity for oil palm landscape restoration. Commun. Earth Environ. 4. https://doi.org/10.1038/s43247-023-00875-6.
Morelli, F., Brlík, V., Benedetti, Y., et al., 2022. Detection rate of bird species and what it depends on: tips for field surveys. Front. Ecol. Evol. 9. https://doi.org/10.3389/fevo.2021.671492.
Nelson D.W., Sommers L.E.1982. Total carbon, organic carbon, and organic matter.
Newbold, T., Hudson, L.N., Hill, S.L.L., et al., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520. https://doi.org/10.1038/nature14324.
Nguyen, A., Tilker, A., Le, Q.T., et al., 2025. Ecotones shape ground-dwelling mammal and bird diversity along a habitat gradient in the southern coastal dry forests of Vietnam. Biotropica 57. https://doi.org/10.1111/btp.13422.
Nobre, A.D., Cuartas, L.A., Hodnett, M., et al., 2011. Height above the nearest drainage - a hydrologically relevant new terrain model. J. Hydrol. (Amst.) 404, 13–29. https://doi.org/10.1016/j.jhydrol.2011.03.051.
Ocampo-Ariza, C., Vansynghel, J., Bertleff, D., et al., 2023. Birds and bats enhance cacao yield despite suppressing arthropod mesopredation. Ecol. Appl. 33. https://doi.org/10.1002/eap.2886.
Pacheco, V., Diaz, S., Graham-Angeles, L., et al., 2021. Updated list of the diversity of mammals from Peru and a proposal for its updating. Rev. Peru. Biol. 28. https://doi.org/10.15381/RPB.V28I4.21019.
Pascual-Hortal, L., Saura, S., 2006. Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landsc. Ecol. 21. https://doi.org/10.1007/s10980-006-0013-z.
Pendrill, F., Gardner, T.A., Meyfroidt, P., et al., 2022. Disentangling the numbers behind agriculture-driven tropical deforestation. Science 377, 1979.
Peri, P.L., Lasagno, R.G., Pastur, G.M., et al., 2019. Soil carbon is a useful surrogate for conservation planning in developing nations. Sci. Rep. 9, 1–6. https://doi.org/10.1038/s41598-019-40741-0.
Perrin, A., Rein, F., Christe, P., Pellet, J., 2025. Habitat fragmentation impact on insect diversity: opposing forces at patch and landscape levels. Landsc. Ecol. 40. https://doi.org/10.1007/s10980-025-02133-w.
Pimm, S.L., Jenkins, C.N., Abell, R., et al., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. Science 344, 1979. https://doi.org/10.1126/science.1246752.
Plenge, M.A., Angulo, F., 2026. Lista de las aves del Perú / List of the birds of Peru. Unión de Ornitólogos del Perú. https://sites.google.com/site/boletinunop/checklist. Accessed 11 Jul 2026.
Potapov, P., Li, X., Hernandez-Serna, A., et al., 2021. Mapping global forest canopy height through integration of GEDI and Landsat data. Remote. Sens. Environ. 253. https://doi.org/10.1016/j.rse.2020.112165.
Priyadarshana, T.S., Martin, E.A., Sirami, C., et al., 2024. Crop and landscape heterogeneity increase biodiversity in agricultural landscapes: A global review and meta-analysis. Ecol. Lett. 27. https://doi.org/10.1111/ele.14412.
Rajaonarimalala, R., Korol, Y., Andrianarimisa, A., et al., 2024. Complex stands in forested tropical landscapes harbor more endemic biodiversity and ecosystem functions. Glob. Ecol. Conserv. 54. https://doi.org/10.1016/j.gecco.2024.e03154.
Santos, P.Z.F., Crouzeilles, R., Sansevero, J.B.B., 2019. Can agroforestry systems enhance biodiversity and ecosystem service provision in agricultural landscapes? A meta-analysis for the Brazilian Atlantic Forest. For. Ecol. Manag. 433, 140–145. https://doi.org/10.1016/j.foreco.2018.10.064.
Shennan-Farpón, Y., Visconti, P., Norris, K., 2021. Detecting ecological thresholds for biodiversity in tropical forests: Knowledge gaps and future directions. Biotropica 53 (5), 1276–1289. https://doi.org/10.1111/btp.12999.
Song, X.P., Hansen, M.C., Stehman, S.V., et al., 2018. Global land change from 1982 to 2016. Nature 560, 639–643. https://doi.org/10.1038/s41586-018-0411-9.
Sousa, T.R., Schietti, J., Ribeiro, I.O., et al., 2022. Water table depth modulates productivity and biomass across Amazonian forests. Glob. Ecol. Biogeogr. 31. https://doi.org/10.1111/geb.13531.
Stein, A., Gerstner, K., Kreft, H., 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol. Lett. 17.

Stork, N.E., Srivastava, D.S., Eggleton, P., et al., 2017. Consistency of effects of tropical-forest disturbance on species composition and richness relative to use of indicator taxa. Conserv. Biol. 31. https://doi.org/10.1111/cobi.12883.

Thorn, S., Bässler, C., Brandl, R., et al., 2018. Impacts of salvage logging on biodiversity: a meta-analysis. J. Appl. Ecol. 55.

Tilman, D., 1982. Resource competition and community structure. Monogr. Popul. Biol. 17. https://doi.org/10.2307/4549.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., et al., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87.

van Dijk, L.J.A., Fisher, B.L., Miraldo, A., et al., 2024. Temperature and water availability drive insect seasonality across a temperate and a tropical region. Proc. R. Soc. B Biol. Sci. 291. https://doi.org/10.1098/rspb.2024.0090.

Vansynghel, J., Ocampo-Ariza, C., Maas, B., et al., 2022a. Quantifying services and disservices provided by insects and vertebrates in cacao agroforestry landscapes. Proc. R. Soc. B Biol. Sci. 289. https://doi.org/10.1098/rspb.2022.1309.

Vansynghel, J., Ocampo-Ariza, C., Maas, B., et al., 2022b. Cacao flower visitation: low pollen deposition, low fruit set and dominance of herbivores. Ecol. Solut. Evid. 3. https://doi.org/10.1002/2688-8319.12140.

Vlam, M., van der Sleen, P., Groenendijk, P., Zuidema, P.A., 2017. Tree age distributions reveal large-scale disturbance-recovery cycles in three tropical forests. Front. Plant. Sci. 7. https://doi.org/10.3389/fpls.2016.01984.

Wang, X., Hua, F., Wang, L., et al., 2019. The biodiversity benefit of native forests and mixed-species plantations over monoculture plantations. Divers. Distrib. 25. https://doi.org/10.1111/ddi.12972.

Willmer, J.N.G., Püttker, T., Prevedello, J.A., 2022. Global impacts of edge effects on species richness. Biol. Conserv. 272. https://doi.org/10.1016/j.biocon.2022.109654.

Wurz, A., Tscharntke, T., Martin, D.A., et al., 2022. Win-win opportunities combining high yields with high multi-taxa biodiversity in tropical agroforestry. Nat. Commun. 13. https://doi.org/10.1038/s41467-022-30866-8.

Xu, L., Saatchi, S.S., Yang, Y., Myneni, R.B., Frankenberg, C., Chowdhury, D., Bi, J., 2015. Satellite observation of tropical forest seasonality: spatial patterns of carbon exchange in Amazonia. Environ. Res. Lett. 10 (8), 084005. https://doi.org/10.1088/1748-9326/10/8/084005.