

Canopy functional composition as an indicator of bird traits, taxonomy, and vulnerability in tropical Peruvian forests

Received: 5 September 2024

Accepted: 14 August 2026

Published online: 25 September 2026

 Check for updatesGeorge Olah¹✉, Maldwyn John Evans¹ & Gregory P. Asner²✉

Tropical forests harbour exceptional biodiversity, yet anthropogenic change is rapidly altering forest composition and structure in ways that shape species' ecological strategies and persistence. While advances in remote sensing now allow detailed characterisation of canopy function, links between forest functional diversity and animal traits remain poorly understood. Here, using linear model selection and variance partitioning, we test whether canopy functional groups (clusters of forest types sharing similar structure, chemistry, and phenology) predict variation in bird community (>1300 species) functional traits, life history traits, vulnerability, and taxonomy across Andean-Amazonian forests in Peru, accounting for a comprehensive baseline of environmental and structural predictors. Distinct forest functional groups are associated with distinct bird traits, levels of anthropogenic impact, and taxonomic assemblages, providing explanatory power beyond traditional abiotic gradients. For example, Southern Amazonian lowlands and Northern Amazonian Swamps contain large-bodied, slow-reproducing, and non-passerine-dominated assemblages. In contrast, Amazonian floodplains support small, fast-reproducing, and passerine-dominated assemblages. These findings underscore the potential of integrating habitat functionality with species traits to map critical resource landscapes and revolutionise conservation prioritisation strategies such as gap analyses.

Functional biogeography describes the geographic distribution of diversity, form, and function¹. Recent advances in remote sensing now allow these functional traits to be measured within and across plant communities, offering unprecedented insight into the functional structure of ecosystems². After detailed calibration, canopy traits such as chemical composition, water content, and leaf mass can be accurately mapped³. Combined with field-based ecological data, forest functional diversity provides further insight into how forest communities are assembled and how they interact with broader biota⁴.

Birds account for approximately 15% of all described vertebrate diversity on Earth⁵, and exhibit disproportionately high species richness in tropical Asia, sub-Saharan Africa, and Central and South

America⁶. Traditionally, large-scale models of avian biodiversity and trait distributions have relied heavily on broad abiotic gradients, utilising standard variables such as climate (temperature and precipitation), topography (elevation and slope), and coarse structural metrics like overall forest cover or canopy height^{6–8}. While these standard biodiversity models successfully capture broad biogeographic turnover, they often treat contiguous forest blocks as functionally uniform, missing the fine-scale chemical and physiological variations that directly dictate local resource availability and habitat quality^{3,9}. Despite being one of the most functionally diverse and well-studied vertebrate groups, forest canopy functional diversity has never been related to bird life-history strategies or conservation vulnerability.

¹Fenner School of Environment and Society, The Australian National University, Canberra, ACT, Australia. ²Center for Global Discovery and Conservation Science, Arizona State University, Hilo, HI, USA. ✉e-mail: george.olah@anu.edu.au; gregasner@asu.edu

Here, we test whether remotely sensed canopy functional groups explain variation in the ecological traits, conservation status, and taxonomy of bird species across the Andean-Amazonian forests of Peru. Peru alone is home to 18% of the world's bird species, including 139 endemics¹⁰, many of which are dependent on forest habitats that cover more than 60% of the country's land area¹¹. Understanding how birds respond to variation in canopy function is especially important in tropical forests, where deforestation and climate change are rapidly altering forest composition and structure. While previous studies have shown that functionally diverse forests tend to be more productive and resilient¹², the role of forest canopies in shaping animal communities, particularly in terms of ecological traits and vulnerability, remains unclear.

From a conservation perspective, it is critically important to understand how animals use remaining habitats and how they might respond to threats. Because canopy functional traits (such as leaf chemistry) determine resource availability (e.g., fruit production, nesting structure)², mapping these traits can reveal the functional carrying capacity of a landscape. Research at the regional level can thus generate better predictions of ecosystem responses to habitat loss¹³ by identifying which forest types harbour the most sensitive life-history strategies (e.g., large-bodied, slow-reproducing species¹⁴) versus those supporting resilient, generalist communities.

Using a comprehensive high-resolution map of forest canopy functional diversity scaled to an entire tropical country², we ask whether different forest functional groups are associated with predictable differences in functional traits of birds, their life history strategies, vulnerability, and taxonomy (Supplementary Table 1). We tested this relationship with over 1300 bird species using ordination and linear model selection (see our simplified modelling framework in Supplementary Table 2). Our findings demonstrate that remotely sensed canopy function can provide insights into the trait structure and vulnerability of tropical bird communities, with implications for monitoring and conservation at landscape scales. Specifically, distinct forest functional groups were associated with different bird traits, patterns of threat exposure, and taxonomic assemblages, establishing broad-scale empirical evidence of how canopy functional diversity relates to avian communities across ecological and evolutionary dimensions.

Results

Functional, ecological, vulnerability, and taxonomic gradients

We identified major ecological and phylogenetic gradients among forest-dependent birds of Peru using principal component analysis (PCA; Fig. 1; Supplementary Data 1–4). For functional traits, PC1 separated large-bodied from small-bodied species across all morphological measurements, PC2 distinguished nocturnal from diurnal species, and PC3 and PC4 captured variation in body proportions and flight morphology, respectively (Fig. 1a, b). For life history traits, PC1 separated understorey from canopy foragers, PC2 reflected life history pace (generation length and clutch size), PC3 contrasted midstory foraging with clutch size, and PC4 captured aerial foraging specialisation (Fig. 1c, d). Vulnerability PC1 represented cumulative exposure to multiple anthropogenic threats, PC2 contrasted pollution and human disturbance with residential development, PC3 distinguished development-type threats from invasive species exposure, and PC4 reflected ecosystem integrity (Fig. 1e, f). For taxonomic composition, PC1 distinguished non-passerines from passerines, with subsequent axes highlighting variation among specialist groups, including hummingbirds (Trochilidae) and nightjars (Caprimulgiformes) on PC2, and tyrant flycatchers (Tyrannidae) versus tanagers (Thraupidae) on PC3 (Fig. 1g, h).

Canopy function explains unique trait variation

We used functional forest maps partitioned into 36 forest functional classes (FFCs; Supplementary Fig. 1) in six groups (FFGs; Fig. 2a; Table 1) that previously showed strong correspondence to tree taxonomic beta

diversity². To evaluate whether FFGs explained bird trait variation independently of landscape-level gradients most likely to covary with forest functional composition, we incorporated seven environmental predictors in our model selection framework (see “Methods”). Top-ranked models demonstrated that FFGs were associated with distinct patterns in bird trait syndromes, threat exposure, and taxonomic structure (Fig. 2; Supplementary Data 5–14), providing explanatory power beyond this environmental baseline. Among the environmental predictors, total insolation and urbanisation were most frequently selected, appearing in 12 and 11 of 16 top-ranked models, respectively. FFGs were informative for 10 of 16 trait axes, increasing the variance explained by the baseline models by 16% to 102% where present (Supplementary Data 14). On four axes, including nocturnality (Functional PC2) and aerial foraging specialisation (Life History PC4), FFG variables did not improve model fits, indicating that not all dimensions of bird trait space are structured by forest functional composition. Where FFGs were informative, their effect sizes were often substantially larger than those of environmental predictors (Fig. 2).

Bird trait syndromes across distinct forest types

The Fitzcarrald Arch of the Southern Amazon (FFG1) was associated with large-bodied birds (Functional PC1, $\beta = 2.84$, $t(1294) = 4.74$, $p < 0.001$, 95% CI = 1.67–4.02) with long generation times and small clutches (Life History PC2, $\beta = 0.63$, $t(1296) = 2.17$, $p = 0.031$, 95% CI = 0.06–1.19). Assemblages were non-passerine dominated (Taxonomy PC1, $\beta = 0.22$, $t(1295) = 4.34$, $p < 0.001$, 95% CI = 0.12–0.32).

The Northern Amazonian lowland forests on low-fertility clay soils (FFG2) were associated with canopy-foraging species (Life History PC1, $\beta = 0.23$, $t(1299) = 6.31$, $p < 0.001$, 95% CI = 0.16–0.3) and development-type threats over pollution and disturbance (Vulnerability PC2, $\beta = -0.45$, $t(1297) = -2.06$, $p = 0.039$, 95% CI = -0.88 to -0.02). Lowland Amazonian floodplains (FFG3) showed the strongest associations with small-bodied birds (Functional PC1, $\beta = -7.22$, $t(1294) = -4.25$, $p < 0.001$, 95% CI = -10.55 to -3.89) and fast life histories, with short generation times and large clutches (Life History PC2, $\beta = -2.07$, $t(1296) = -2.52$, $p = 0.012$, 95% CI = -3.68 to -0.45; Life History PC3, $\beta = 2.6$, $t(1296) = 2.61$, $p = 0.009$, 95% CI = 0.65–4.55). FFG3 was also associated with elevated pollution and disturbance threats (Vulnerability PC2, $\beta = 0.59$, $t(1297) = 2.68$, $p = 0.007$, 95% CI = 0.16–1.02) and passerine-dominated assemblages and aerial foragers (Taxonomy PC1, $\beta = -0.66$, $t(1295) = -4.66$, $p < 0.001$, 95% CI = -0.94 to -0.38; Taxonomy PC4, $\beta = 0.03$, $t(1297) = 2.60$, $p = 0.009$, 95% CI = 0.01–0.05).

The colluvial lower Andes (FFG4) were associated with flight-adapted morphology (Functional PC4, $\beta = 1.1$, $t(1296) = 3.41$, $p < 0.001$, 95% CI = 0.47–1.74), small clutch sizes (Life History PC3, $\beta = -2.07$, $t(1296) = -2.67$, $p = 0.008$, 95% CI = -3.59 to -0.55), and elevated multi-threat exposure (Vulnerability PC1, $\beta = 1.15$, $t(1295) = 2.78$, $p = 0.005$, 95% CI = 0.34–1.96).

The Northern Amazon swamp forests (FFG5) communities were dominated by very large-bodied, terrestrially foraging birds (Functional PC1, $\beta = 9.48$, $t(1294) = 3.49$, $p < 0.001$, 95% CI = 4.16–14.8; Functional PC4, $\beta = -2.51$, $t(1296) = -3.43$, $p < 0.001$, 95% CI = -3.94 to -1.07) with slow life histories (Life History PC2, $\beta = 3.67$, $t(1296) = 2.79$, $p = 0.005$, 95% CI = 1.09–6.25). FFG5 showed reduced overall threat exposure (Vulnerability PC1, $\beta = -1.36$, $t(1295) = -3.29$, $p = 0.001$, 95% CI = -2.17 to -0.55) and strong non-passerine dominance (Taxonomy PC1, $\beta = 1.09$, $t(1295) = 4.75$, $p < 0.001$, 95% CI = 0.64–1.54).

The submontane and montane Andes (FFG6) showed smaller-bodied, flight-adapted species (Functional PC1, $\beta = -4.65$, $t(1294) = -2.81$, $p = 0.005$, 95% CI = -7.9 to -1.4; Functional PC3, $\beta = 0.27$, $t(1298) = 2.35$, $p = 0.019$, 95% CI = 0.05–0.5; Functional PC4, $\beta = 1.34$, $t(1296) = 2.97$, $p = 0.003$, 95% CI = 0.46–2.23) with fast life histories (Life History PC2, $\beta = -2.14$, $t(1296) = -2.66$, $p = 0.008$, 95% CI = -3.72 to -0.57) and with more passerines (Taxonomy PC1, $\beta = -0.62$, $t(1295) = -4.38$, $p < 0.001$, 95% CI = -0.9 to -0.34).

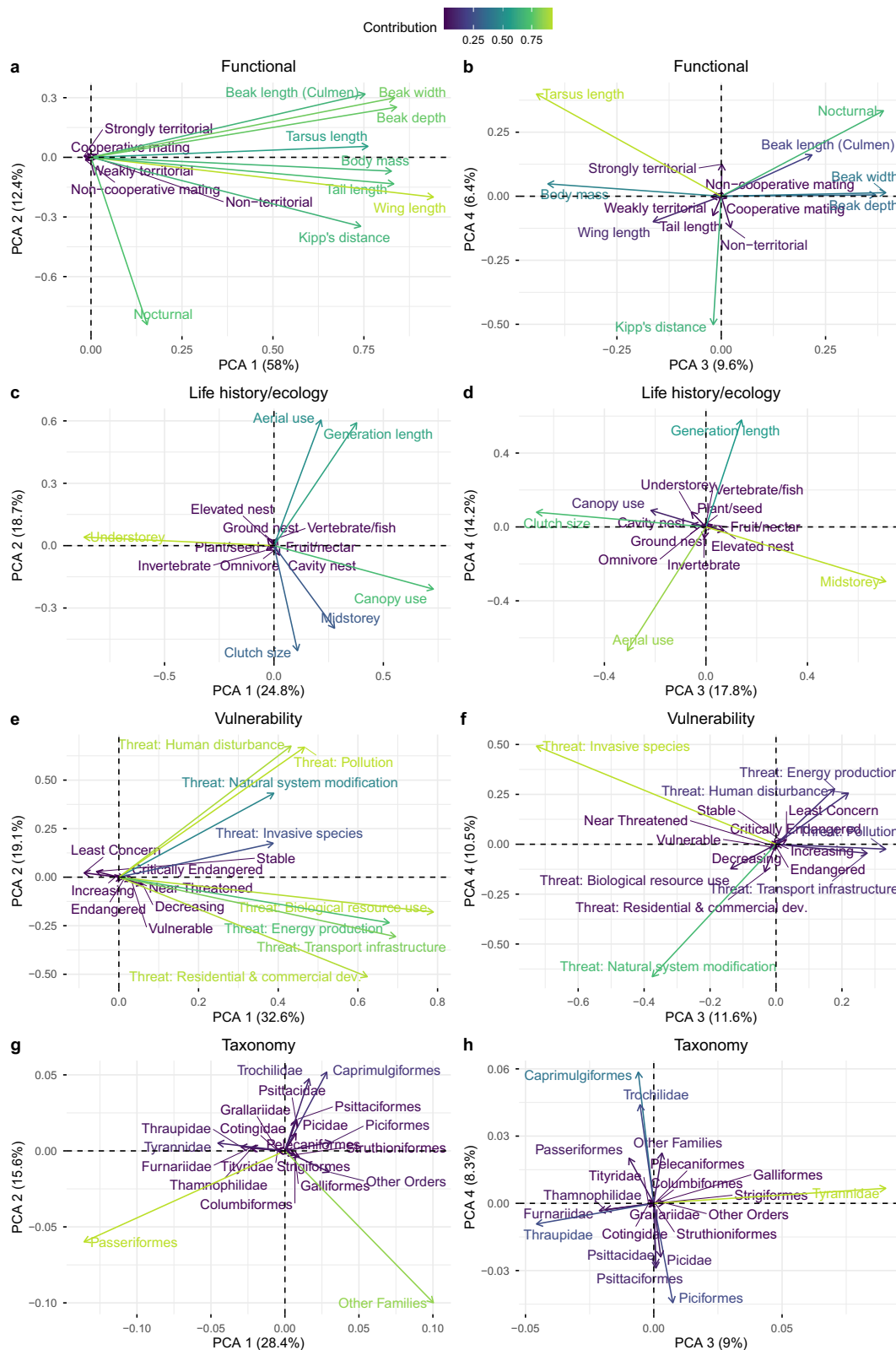


Fig. 1 | Multidimensional trait, threat, and taxonomic variation in Peruvian forest-dependent birds. Principal component analysis (PCA) biplots illustrating the first four axes of variation for functional traits (a, b), life history traits (c, d),

vulnerability (e, f), and taxonomy (g, h) across forest-dependent bird species in Peru. The colour of the arrows and variable names represent their contribution (blue indicates lower and yellow indicates higher contribution).

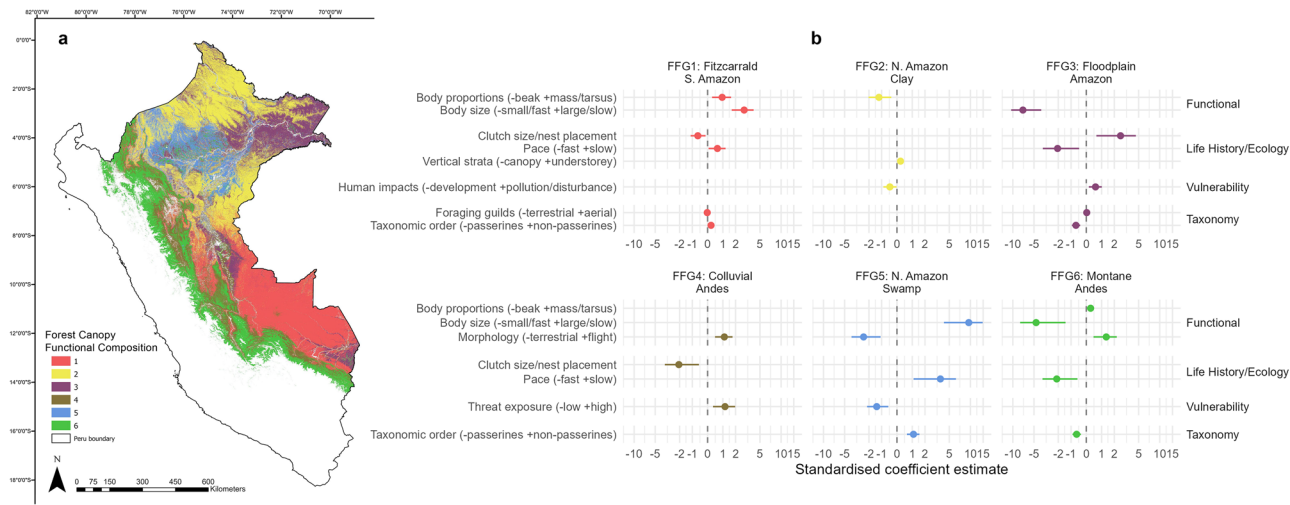


Fig. 2 | Forest canopy functional diversity of Peru in relation to bird traits. **a** Map indicates the distribution of six forest functional groups (FFG) by different colours (red = FFG1, yellow = FFG2, purple = FFG3, brown = FFG4, blue = FFG5, green = FFG6). Map was created using QGIS v3.3. See Supplementary Fig. 1 for parallel map of 36 forest functional classes. **b** Coefficient estimates from top-ranked linear models linking forest functional group composition (shown by the same colour codes as on the map) to bird functional and life history traits, vulnerability, and taxonomic structure. Each row shows a PCA axis (response), and estimates indicate

the direction and uncertainty of association with each of six forest functional groups. Points represent mean estimates ($n = 1303$ bird species) and lines indicate 95% confidence intervals (see Supplementary Data 13 for values). The x-axis is plotted on a log scale to aid visual interpretation. Only predictors that were retained in the most parsimonious model in each model selection set are plotted. The retained environmental predictors (including elevation, cloud cover, urbanisation, aboveground carbon density, bare substrate, photosynthetic vegetation, and solar insolation) are not shown (see Supplementary Fig. 3).

Table 1 | Ecological summary of forest functional groups (FFGs) and their relevance for bird trait patterns

FFG	Name	Key features	Implications for bird assemblages
FFG1	Fitzcarrald South Amazon	Southern Amazonian lowlands (Fitzcarrald Arch); high canopy foliar N; low defence compounds.	Large-bodied birds with long generation times and small clutches. Non-passerine-dominated assemblages.
FFG2	North Amazon Clay	Northern Amazonian lowlands; very low-fertility clay soils; low foliar P and Ca; high phenol- and lignin-based defences.	Canopy-foraging species primarily impacted by development-type threats rather than pollution and disturbance.
FFG3	Floodplain Amazon	Lowland Amazonian floodplains; high rock-derived cation deposition.	Small-bodied birds with fast life histories (short generation times and large clutches). Threatened by pollution and disturbance. Passerine-dominated assemblages and aerial foragers.
FFG4	Colluvial Andes	P-rich colluvial deposition zones at the base of the Andes.	Birds with flight-adapted morphology and small clutch sizes. Assemblages face elevated exposure to multiple threats.
FFG5	North Amazon Swamp	Anoxic swamp regions (Pastaza-Maranon foreland); low canopy foliar N and P; high defences.	Very large-bodied, terrestrially foraging birds with slow life histories. Reduced overall threat exposure. Non-passerine dominance.
FFG6	Montane Andes	Submontane to montane Andes; high leaf mass per area (LMA) and leaf water content; low foliar N and Ca.	Smaller-bodied, flight-adapted birds with fast life histories. Passerine-dominated assemblages.

Each FFG represents a cluster of forest types sharing similar canopy chemical and structural traits, derived from high-resolution airborne remote sensing⁷. The table summarises their key ecological features and observed associations with bird functional traits, threat exposure, and taxonomic structure, based on our multivariate analysis.

Species richness varied moderately among forest functional groups, ranging from 1269 species in FFG1 to 1383 in FFG5, with a mean of 1344 ± 41.5 . The spatial distribution of total, non-threatened, and threatened species richness across Peru is shown in Supplementary Fig. 2.

Discussion

Our study provides spatially explicit evidence that forest canopy functional diversity is linked to major gradients of functional, ecological, vulnerability-related, and taxonomic trait diversity in forest-dependent birds of Peru. By combining remote sensing of forest functional groups (FFGs) with trait-based and taxonomic data from over 1300 bird species, we uncovered consistent associations between forest canopy composition and bird trait syndromes, revealing that functionally distinct forest canopy groups support bird assemblages with characteristic morphologies, life history strategies, conservation vulnerabilities, and evolutionary lineages. Our model selection framework, incorporating seven environmental predictors including

canopy biomass, urbanisation, bare substrate, and solar insolation, demonstrated that FFGs provide explanatory power beyond a broad range of environmental gradients. Variance partitioning confirmed that FFGs increased the baseline explained variance by 16% to 102% on axes where they were informative, and FFG effect sizes were often substantially larger than those of environmental predictors. This suggests that forest functional composition exerts influence on bird trait distributions that cannot be reduced to the underlying environmental gradients that drive canopy composition itself.

We selected birds as our model taxa, as they are among the best understood vertebrates with regard to ecology and conservation status⁵, and because many bird species are tied to forest habitat. Specific forest functional groups (defined by differences in canopy chemistry, structure, and resource availability) were associated with bird trait PCs that captured major ecological dimensions, such as body size, life history pace, foraging strata, and threat exposure. Birds inhabiting the Fitzcarrald Southern Amazon (FFG1) and northern Amazonian swamp forests (FFG5) tended to be larger-bodied and longer-lived species,

traits associated with slower reproductive strategies and increased vulnerability. Conversely, floodplain Amazon (FFG3) and montane Andean forests (FFG6) were associated with smaller-bodied, faster-reproducing species, which may reflect different resource availability and environmental constraints. These patterns suggest that variation in forest functional composition is mirrored by shifts in avian functional niches, consistent with niche assembly processes linking habitat traits to species' life-history strategies¹⁵.

Associations between forest function and anthropogenic threats were also evident. Northern Amazonian swamp forests (FFG5) showed reduced overall multi-threat exposure, though they were also associated with elevated invasive species and ecosystem integrity threats. Floodplain forests (FFG3) were associated with greater exposure to pollution and human disturbance. These results indicate that remotely sensed canopy traits offer a granular yet scalable means to identify distinct conservation risk profiles across forest types. Conserving functionally diverse forests remains essential not only for maintaining tree diversity but also for sustaining the range of bird life-history strategies that underpin ecosystem functioning^{16,17}.

The taxonomic composition of bird communities also varied systematically across forest functional groupings. Passerine-dominated assemblages were associated with Amazonian floodplain forests (FFG3) and Andean submontane and montane forests (FFG6). Non-passerine dominance was strongest in Northern Amazonian swamp forests (FFG5), with weaker non-passerine enrichment also evident in the Southern Amazonian Fitzcarrald Arch (FFG1). Both FFG5 and FFG1 exhibit distinct chemical profiles and hydrological regimes. These taxonomic patterns may reflect long-term evolutionary filtering, where distinct forest resource profiles select for lineages with corresponding physiological or foraging adaptations^{18,19}. Such alignment between taxonomic and forest functional composition underscores the role of habitat heterogeneity in shaping community assembly across ecological and phylogenetic dimensions.

Our canopy trait data, though derived from airborne spectroscopy with high spatial and spectral resolution, aggregate functional properties across 1-ha grid cells, which may not align with the fine spatial scales at which individual birds select resources or territories²⁰. As with any remote sensing-based study, limitations include potential noise introduced by atmospheric variation, sensor calibration, and uncertainty in chemical trait retrievals²¹. Furthermore, linking gridded environmental data to broad species range polygons inherently masks local dynamics, such as biotic interactions or micro-habitat selection. Consequently, the absolute variance explained by broad-scale macroecological models is often modest, reflecting the high intrinsic noise of such datasets²². However, these challenges are partly mitigated by calibrating trait maps to extensive field plots² and averaging trait values over species' distributions to reduce local variance. Importantly, variance partitioning against our comprehensive environmental baseline confirmed that within the explainable variance, canopy functional traits provide complementary information beyond a broad range of environmental gradients. FFGs represent emergent multivariate ecosystem properties rather than direct expressions of isolated environmental covariates²³. The emergence of consistent, ecologically interpretable associations between specific forest functional groups and distinct bird trait syndromes strengthens the case for integrating canopy trait data into biodiversity monitoring and conservation planning.

Peru hosts a large proportion of the earth's biodiversity^{24,25}, which is being lost at an accelerating rate²⁶. Given that Peru is also the second richest country in bird diversity worldwide (after Colombia), and 80% of its bird species are dependent on forest habitat, our findings have clear implications for conservation. Forests with distinct canopy functional traits provide different ecological opportunities and constraints for birds. Mapping and monitoring these functional traits remotely offer a scalable way to identify potential associations between forest composition and avian trait structure, rather than

direct community responses. Importantly, such trait-based frameworks complement field-based studies by highlighting where functional shifts in canopy composition are most likely to influence the structure and vulnerability of bird assemblages.

Given the demonstrated linkages between forest function and bird ecology in Peru, these insights may prove equally valuable in other biodiverse tropical regions. More broadly, the approach demonstrated here could support expanded biodiversity monitoring across the entire Amazon Basin, particularly if combined with emerging satellite-based imaging spectroscopy from missions such as ESA CHIME²⁷, NASA SBG²⁸, and Planet Tanager (G. Asner, pers. comm.). Although these missions will not capture forest structure directly, their broad coverage could complement available spaceborne LiDAR²⁹ and high-resolution mapping tools to extend trait–biodiversity analyses across regions with limited ground data. We view this study on Peru as a proof of concept for linking canopy functional diversity to animal trait structure, with potential for application throughout global tropical forests.

Our results suggest that these canopy chemical and physiological forest maps can serve as a critical layer for conservation gap analyses. For example, we show that Northern Amazonian swamp forests (FFG5) uniquely support assemblages of large-bodied, evolutionarily distinct non-passerines. If conservation networks prioritise areas based solely on species richness or generic forest cover, they may inadvertently protect resilient floodplain forests (FFG3)—which are dominated by small-bodied, fast-reproducing species—while leaving these functionally unique and vulnerable assemblages (in FFG5) unprotected, potentially risking the loss of critical ecosystem services like large-seed dispersal. Therefore, while our goal was not to delineate specific boundaries of protected areas, we demonstrate that stratifying conservation planning by forest functional groups is essential to safeguard the full spectrum of avian ecological roles, preventing the silent loss of functional diversity even where forest cover remains intact.

Methods

Trait database construction

We first assembled a database of all extant bird species of Peru using the global database of HBW and BirdLife International³⁰, which provides standardised global taxonomy, International Union for Conservation of Nature's (IUCN) Red List categories, and vulnerability data for all bird species. We evaluated the bird list by consulting with the Committee of Peruvian Bird Records (Comité de Registros de Aves Peruanas), after which we excluded species with no real Peruvian distribution and included birds recently reported for Peru, resulting in 1893 bird species. Of these, we used data on 1492 species that are forest-dependent to some degree. We excluded non-forest-dependent birds because their ecological distributions are shaped by habitat variables not captured by forest canopy traits (e.g., open grassland, wetland, desert), making them less suitable for evaluating canopy–trait associations. We obtained morphological trait data (body mass, beak dimensions, wing length, tarsus length, tail length, and Kipp's distance) from the AVONET database³¹, a comprehensive functional trait dataset for all birds containing measurements from over 90,000 individuals. In total, we used 32 variables for each species (Supplementary Table 1). Our database contained the IUCN Red List assessment of each species in the following categories: Least Concern, Near Threatened, Vulnerable, Endangered, Critically Endangered, and Data Deficient.

Remote sensing data

The Global Airborne Observatory, formerly the Carnegie Airborne Observatory^{32,33}, was developed for remote mapping of ecosystems at the macroscale³⁴. The airborne observatory is equipped with a combination of state-of-the-art sensors including a visible-to-shortwave infrared imaging spectrometer, waveform light detection and ranging scanner, and visible-to-near infrared imaging spectrometer³². Data from these instruments are integrated on-board using fusion

techniques, providing a unique combination of information on forest canopy structure, chemistry, and biodiversity^{2,35,36}.

Asner et al.² mapped the Peruvian Andes and Amazon forest for seven canopy traits (foliar nitrogen, water, phosphorus, calcium, polyphenols, lignin, and leaf mass per unit area), alongside additional structural data. Using cluster analysis, they assigned the measured traits into 36 forest functional classes (FFC; Supplementary Fig. 1), representing coexistent species with similar functional traits, and then clustered these FFCs into six forest functional groups (FFG; Fig. 1). The clustering of FFCs and FFGs was based on unsupervised classification of field-calibrated canopy trait maps², not on supervised predictive modeling, and thus is not subject to spatial overfitting issues³⁷.

We used the geographic distribution available for 1470 forest-dependent bird species³⁸ to calculate spatial statistics, excluding those without polygon data. We overlaid the species range polygons with the remotely sensed environmental data previously published by the Global Airborne Observatory⁴. We calculated class membership statistics of the FFG maps within the ranges of individual bird species in QGIS v3.3 (www.qgis.org). For each species, we extracted the total area (in ha) occupied within each of the six FFG categories and used these values in the subsequent analysis.

We used the broader FFGs rather than the original 36 FFCs to reduce model dimensionality and to improve ecological interpretability, as previously established². These aggregated groups reflect multivariate structure in canopy functional traits that arise from the combined influence of substrate geology, soil properties, hydrology, and climate rather than any single environmental gradient, and have been validated as meaningful forest types across Peru²³. While these traits represent aggregate pixel-level values rather than individual tree measurements, they reflect the dominant functional signatures of plant assemblages at a resolution widely adopted in landscape ecology. We acknowledge that the bird assemblages inferred from the overlapping polygon range maps may not capture local abundance or precise species presence. As such, these assemblages represent broad-scale, modeled estimates rather than direct field observations, and results should be interpreted considering this inherent uncertainty. Despite these limitations, using polygon-based assemblages remains a widely accepted approach for broad-scale ecological analyses, particularly when comprehensive field data are unavailable at national extents³⁹.

In addition to forest functional group metrics, we extracted seven environmental predictors for each species, each calculated as the area-weighted mean across each species' range polygon. We derived elevation (m above sea level at 90 m resolution) from a digital elevation model⁴⁰, and calculated the mean elevation by the area occupied within each species' range polygon. We obtained cloud cover from MODIS (NASA Moderate Resolution Imaging Spectroradiometer), representing the proportion of observations with cloud presence². As a proxy for canopy biomass and structure, we derived aboveground carbon density (ACD, Mg C ha⁻¹) from the Global Airborne Observatory dataset³⁶. We quantified urbanisation as the log-transformed mean night light emission intensity (DMSP/VIIRS)⁴¹. We also extracted bare substrate cover, photosynthetically active vegetation (PAV) cover, and total solar insolation (kWh m⁻² at the summer solstice) from the Global Airborne Observatory dataset². We standardised all predictors (mean = 0, SD = 1) prior to analysis.

Data analysis

We used R v4.3.2⁴² for data analysis and visualisation, with the packages of 'tidyverse' v2⁴³ for data manipulation, 'car' v3.1.2⁴⁴ for regression, 'parallel' v4.2 for parallel processing, 'forcats' v1⁴⁵ for factor manipulation, 'ggpubr' v0.6⁴⁶ for plot arrangement, 'patchwork' v0.1⁴⁷ for panel stacking, 'flextable' v0.9.2⁴⁸ for table formatting, and 'officer' v0.6.2⁴⁹ for Word document export.

We explored how forest functional groups related to bird species' functional traits, life history traits, conservation status, and taxonomy

using ordination and linear model selection using Akaike's Information Criterion for small sample sizes (AICc)⁵⁰. We excluded species with missing values in any of the selected functional, threat, or taxonomic variables to ensure consistent input across analyses. This left 1303 forest-dependent bird species with complete trait records. For each species, we assembled four groups of variables (Supplementary Table 1): functional traits (e.g., body mass, body measurements), life history traits (e.g., clutch size, diet, foraging strategies), vulnerability attributes (e.g., IUCN category, population trend, presence of specific threats), and taxonomic identity (order and family).

Because many ecological traits covary, we used principal components analyses (PCA) to reduce dimensionality and focus on major ecological gradients, which we then modelled as multivariate responses. We transformed categorical predictors into scaled binary variables, adjusting for the number of factor levels, and standardised continuous traits with 'FactoMineR' v2.8⁵¹. We then carried out separate PCA for each trait group using the 'prcomp' function in R⁴². From each PCA, we retained the first four axes, which captured the main gradients of variation in each of the groups of traits, and visualised with 'factoextra' v1.0.7⁵² (see Fig. 1, Supplementary Data 1–4).

We included seven environmental predictors in our model selection framework. Elevation is a fundamental environmental gradient in montane tropical systems, acting as a proxy for temperature and related climatic factors that strongly structure avian communities along Andean slopes^{53,54}. Cloud cover represents an independent moisture gradient particularly important in tropical montane systems⁵⁵. Cloud forests, characterised by persistent low-level cloud cover, provide substantial water inputs through fog drip and create distinct microclimatic conditions that support specialised, highly endemic fauna, with over one-third of Peru's endemic birds, mammals, and frogs restricted to cloud forest habitats⁵⁵. We used aboveground carbon density (ACD) as a proxy for canopy biomass and structural complexity. We included urbanisation (night light emissions), bare substrate cover, photosynthetically active vegetation cover, and total solar insolation to capture landscape-level disturbance and productivity gradients. Together, these predictors represent the major environmental axes most likely to covary with forest functional composition, allowing us to evaluate whether FFGs provide explanatory power independently of this broad environmental baseline.

We used 'glmmTMB' v1.1.7⁵⁶ to fit sets of linear models with Gaussian errors, treating the retained principal component (PC) scores as continuous responses. For each trait group (functional, life history, vulnerability, taxonomy), we conducted information-theoretic multi-model inference on the first four PC axes. For each PC axis, we first fitted all possible subset combinations of the seven environmental predictors using the 'dredge' function from the 'MuMIn' package v1.47.5⁵⁷. This candidate model set established the baseline model of the environmental variables that explained bird traits (PC axes). This full model was:

$$PC_{ij} = \beta_{0j} + \beta_{1j} \cdot Elev_i + \beta_{2j} \cdot Cloud_i + \beta_{3j} \cdot ACD_i + \beta_{4j} \cdot Urban_i + \beta_{5j} \cdot Bare_i + \beta_{6j} \cdot PAV_i + \beta_{7j} \cdot Sol_i + \epsilon_{ij} \quad (1)$$

where PC_{ij} is the score of species i on principal component axis j ; β_{0j} is the intercept for axis j ; β_{1j} to β_{7j} are coefficients for relative elevation ($Elev_i$), cloud cover ($Cloud_i$), aboveground carbon density (ACD_i), urbanisation ($Urban_i$), bare substrate cover ($Bare_i$), photosynthetically active vegetation cover (PAV_i), and total solar insolation (Sol_i), respectively, each standardised to mean = 0, SD = 1; and $\epsilon_{ij} \sim N(0, \sigma_j^2)$ represents normally distributed residuals with variance σ_j^2 estimated separately for each axis. We used linear model selection by Akaike's Information Criterion for small sample sizes (AICc)⁵⁰, fitting all combinations of the environmental predictors, and selecting the top-ranked model as the model to take forward into the next step. For each response variable, we then used their top-ranked baseline model as the basis to test whether the FFG variables provided more explanatory

power above the environmental variables. For each PC axis response, this model was:

$$PC_{ij} = \beta_{0j} + \beta_{1j} \cdot FFG_{1i} + \beta_{2j} \cdot FFG_{2i} + \beta_{3j} \cdot FFG_{3i} + \beta_{4j} \cdot FFG_{4i} + \beta_{5j} \cdot FFG_{5i} + \beta_{6j} \cdot FFG_{6i} + \beta_{ej} \cdot Environmental_i + \varepsilon_{ij} \quad (2)$$

where PC_{ij} is the score of species i on principal component axis j ; β_{0j} is the intercept for axis j ; β_{1j} to β_{6j} are coefficients for the six FFG variables, where FFG_{ki} represents the standardised proportional area of the k^{th} FFG for species i ; β_{ej} are the environmental coefficients from the previous step, each standardised as previously. We then used AICc model selection, holding the environmental variables fixed as the baseline predictors, to test whether adding the FFG variables added predictive power beyond what was explained by environmental variables. Finally, to identify the absolute most parsimonious combination of predictors overall, we generated a full model suite where all thirteen predictors (seven environmental variables and six FFGs) were allowed to compete simultaneously.

To quantify the contribution of FFGs to explained variance independently of environmental predictors, we compared the R^2 from the top-ranked model to that from the baseline model with FFG predictors excluded. We provide model selection tables (Supplementary Data 5–12), top-ranked model coefficient estimates with unconditional standard errors and 95% confidence intervals (Supplementary Data 13), and the variance partitioning results (Supplementary Data 14) in the supplementary materials. A simplified modelling framework is available in Supplementary Table 2.

To evaluate the representativeness and ecological reliability of bird assemblages across FFGs, we calculated species richness for each FFG as the total number of forest-dependent species overlapping with its mapped extent. Spatial patterns of overall, non-threatened, and threatened bird richness were visualised across Peru (Supplementary Fig. 2).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All derived analytical data generated during this study (including principal component loadings, comprehensive model selection tables, model summaries, and variance partitioning results) are provided in the Supplementary Data 1–14. FFC and FFG maps are available in GeoTIFF format at <https://zenodo.org/records/4602641>. Bird range polygons and the trait database used in this study are available at Figshare: <https://doi.org/10.6084/m9.figshare.12894230>. The sources of raw datasets analysed (detailed in Methods and Supplementary Table 1) are available from public repositories, including BirdLife DataZone (<https://datazone.birdlife.org>), AVONET (<https://figshare.com/s/b990722d72a26b5bfead>), Tobias & Pigot (2019; <https://doi.org/10.1098/rstb.2019.0012>), and EltonTraits 1.0 (<https://doi.org/10.6084/m9.figshare.c.3306933>).

Code availability

R code used to generate results are available at Figshare: <https://doi.org/10.6084/m9.figshare.12894230>.

References

- Violle, C., Reich, P. B., Pacala, S. W., Enquist, B. J. & Kattge, J. The emergence and promise of functional biogeography. *Proc. Natl. Acad. Sci.* **111**, 13690–13696 (2014).
- Asner, G. P. et al. Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. *Science* **355**, 385–389 (2017).
- Asner, G. P. et al. Spectroscopy of canopy chemicals in humid tropical forests. *Remote Sens. Environ.* **115**, 3587–3598 (2011).
- Asner, G. P. et al. Targeted carbon conservation at national scales with high-resolution monitoring. *Proc. Natl. Acad. Sci.* **111**, E5016–E5022 (2014).
- BirdLife International. IUCN Red List for birds. Downloaded from <https://datazone.birdlife.org> 05 May 2025. <https://www.iucnredlist.org> (2025).
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
- Elith, J. & Leathwick, J. R. Species Distribution Models: Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Syst.* **40**, 677–697 (2009).
- Davies, R. G. et al. Topography, energy and the global distribution of bird species richness. *Proc. Biol. Sci.* **274**, 1189–1197 (2007).
- Gaston, K. J. Global patterns in biodiversity. *Nature* **405**, 220–227 (2000).
- BirdLife International. Country profile: Peru. Available at <http://datazone.birdlife.org/country/peru>. Accessed: 15 Jun 2024. (2024).
- Global Forest Watch. Dashboard: Peru. Available at <https://www.globalforestwatch.org/dashboards/country/PER>. Accessed: 2024-06-15. www.globalforestwatch.org (2024).
- Schneider, F. D. et al. Mapping functional diversity from remotely sensed morphological and physiological forest traits. *Nat. Commun.* **8**, 1441 (2017).
- Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annu. Rev. Ecol. Syst.* **41**, 321–350 (2010).
- Vergara-Tabares, D. L., Cordier, J. M., Landi, M. A., Olah, G. & Nori, J. Global trends of habitat destruction and consequences for parrot conservation. *Glob. Change Biol.* **26**, 4251–4262 (2020).
- Fussmann, G. F., Loreau, M. & Abrams, P. A. Eco-evolutionary dynamics of communities and ecosystems. *Funct. Ecol.* **21**, 465–477 (2007).
- Tracewski, L. et al. Toward quantification of the impact of 21st-century deforestation on the extinction risk of terrestrial vertebrates. *Conserv. Biol.* **30**, 1070–1079 (2016).
- Olah, G. et al. Ecological and socio-economic factors affecting extinction risk in parrots. *Biodivers. Conserv.* **25**, 205–223 (2016).
- Price, T. D. et al. Niche filling slows the diversification of Himalayan songbirds. *Nature* **509**, 222–225 (2014).
- Pigot, A. L. et al. Macroevolutionary convergence connects morphological form to ecological function in birds. *Nat. Ecol. Evol.* **4**, 230–239 (2020).
- Tobias, J. A., Ottenburghs, J. & Pigot, A. L. Avian diversity: Speciation, macroevolution, and ecological function. *Annu. Rev. Ecol. Syst.* **51**, 533–560 (2020).
- Asner, G. P., Martin, R. E., Anderson, C. B. & Knapp, D. E. Quantifying forest canopy traits: Imaging spectroscopy versus field survey. *Remote Sens. Environ.* **158**, 15–27 (2015).
- Møller, A. & Jennions, M. D. How much variance can be explained by ecologists and evolutionary biologists? *Oecologia* **132**, 492–500 (2002).
- Asner, G. P. et al. Landscape biogeochemistry reflected in shifting distributions of chemical traits in the Amazon forest canopy. *Nat. Geosci.* **8**, 567–573 (2015).
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B. & Kent, J. Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
- Tuomisto, H. et al. Dissecting Amazonian biodiversity. *Science* **269**, 63–66 (1995).
- Pimm, S. L. et al. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752–1–10 (2014).

27. Rast, M., Nieke, J., Adams, J., Isola, C. & Gascon, F. Copernicus Hyperspectral Imaging Mission for the Environment (Chime). In *2021 IEEE International Geoscience and Remote Sensing Symposium IGARSS 108–111*, <https://doi.org/10.1109/IGARSS47720.2021.9553319> (2021).
28. Cawse-Nicholson, K. et al. NASA's surface biology and geology designated observable: A perspective on surface imaging algorithms. *Remote Sens. Environ.* **257**, 112349 (2021).
29. Potapov, P. et al. Mapping global forest canopy height through integration of GEDI and Landsat data. *Remote Sens. Environ.* **253**, 112165 (2021).
30. HBW and BirdLife International. Handbook of the Birds of the World and BirdLife International digital checklist of the birds of the world. **9**. Available at: http://datazone.birdlife.org/userfiles/file/Species/Taxonomy/HBW-BirdLife_Checklist_v9_Oct24.zip (2024).
31. Tobias, J. A. et al. AVONET: morphological, ecological and geographical data for all birds. *Ecol. Lett.* **25**, 581–597 (2022).
32. Asner, G. P. et al. Carnegie Airborne Observatory-2: Increasing science data dimensionality via high-fidelity multi-sensor fusion. *Remote Sens. Environ.* **124**, 454–465 (2012).
33. Asner, G. P., Llactayo, W., Tupayachi, R. & Luna, E. R. Elevated rates of gold mining in the Amazon revealed through high-resolution monitoring. *Proc. Natl. Acad. Sci.* **110**, 18454–18459 (2013).
34. Asner, G. P. & Martin, R. E. Spectral and chemical analysis of tropical forests: Scaling from leaf to canopy levels. *Remote Sens. Environ.* **112**, 3958–3970 (2008).
35. Asner, G. P., Knapp, D. E., Balaji, A. & Paez-Acosta, G. Automated mapping of tropical deforestation and forest degradation: CLASlite. *J. Appl. Remote Sens.* **3**, 033543 (2009).
36. Asner, G. P. et al. High-resolution mapping of forest carbon stocks in the Colombian Amazon. *Biogeosciences* **9**, 2683–2696 (2012).
37. Ploton, P. et al. Spatial validation reveals poor predictive performance of large-scale ecological mapping models. *Nat. Commun.* **11**, 4540 (2020).
38. BirdLife International and HBW. Bird species distribution maps of the world. Available at <http://datazone.birdlife.org/species/requestdis> (2021).
39. Hurlbert, A. H. & Jetz, W. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proc. Natl. Acad. Sci.* **104**, 13384–13389 (2007).
40. NASA JPL. Shuttle Radar Topography Mission (STRM) Global 1 arc second. Available at <https://doi.org/10.5067/MEASURES/SRTM/SRTMGL1.003> (2013).
41. Tobias, J. A. & Pigot, A. L. Integrating behaviour and ecology into global biodiversity conservation strategies. *Philos. Trans. R. Soc. B: Biol. Sci.* **374**, 20190012 (2019).
42. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <https://www.R-project.org> (2026).
43. Wickham, H. et al. Welcome to the tidyverse. *J. Open Source Softw.* **4**, 1686 (2019).
44. Fox, J. & Weisberg, S. *An R Companion to Applied Regression*. Thousand Oaks, CA, USA (Sage, 2019).
45. Wickham, H. *Forcats: Tools for Working with Categorical Variables (Factors)*. Available at <https://forcats.tidyverse.org> (2025).
46. Kassambara, A. *Ggpubr: 'ggplot2' Based Publication Ready Plots*. Available at <https://rpkgs.datanovia.com/ggpubr> (2026).
47. Pedersen, T. L. *Patchwork: The Composer of Plots*. Available at <https://patchwork.data-imaginist.com> (2025).
48. Gohel, D. & Skintzos, P. *Flextable: Functions for Tabular Reporting*. Available at <https://ardata-fr.github.io/flextable-book> (2026).
49. Gohel, D., Moog, S. & Heckmann, M. *Officer: Manipulation of Microsoft Word and PowerPoint Documents*. Available at <https://ardata-fr.github.io/officerverse> (2026).
50. Burnham, K. P. & Anderson, D. R. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. (Springer, 2002).
51. Lê, S., Josse, J. & Husson, F. FactoMineR: An R package for multi-variate analysis. *J. Stat. Softw.* **25**, 1–18 (2008).
52. Kassambara, A. & Mundt, F. *Factoextra: Extract and Visualize the Results of Multivariate Data Analyses*. Available at <https://CRAN.R-project.org/package=factoextra> (2026).
53. Patterson, B. D., Stotz, D. F., Solari, S., Fitzpatrick, J. W. & Pacheco, V. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *J. Biogeogr.* **25**, 593–607 (1998).
54. Kattan, G. H. & Franco, P. Bird diversity along elevational gradients in the Andes of Colombia: Area and mass effects. *Glob. Ecol. Biogeogr.* **13**, 451–458 (2004).
55. Foster, P. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Sci. Rev.* **55**, 73–106 (2001).
56. Brooks, M. E. et al. glmmTMB balances speed and flexibility among packages for Zero-inflated Generalized Linear Mixed Modeling. *R. J.* **9**, 378–400 (2017).
57. Bartoń, K. *MuMIn: Multi-Model Inference*. Available at <https://CRAN.R-project.org/package=MuumIn> (2025).

Acknowledgements

We thank N. Vaughn for processing the GIS data; E. Shafron for visualising some results; M. Plenge for advice on the species list construction; R. Heinsohn, A. L. Smith, and R. Peakall for their comments on the manuscript.

Author contributions

G.O. and G.P.A. conceived the work and acquired funding. M.J.E. and G.O. selected the methodology, conducted the analyses, and visualised the results. G.P.A. supervised and administered the project. G.O. and G.P.A. wrote the original draft, and all authors contributed to editing and reviewing the final paper.

Funding

G.P.A. was supported by the John D. and Catherine T. MacArthur Foundation (grant number 11-99607). G.O. was funded by Australian Research Council DECRA Fellowship (grant number DE230100085) and the Loro Parque Fundación (grant number PP-250-2024). M.J.E. declares no relevant funding.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41467-026-77135-6>.

Correspondence and requests for materials should be addressed to George Olah or Gregory P. Asner.

Peer review information *Nature Communications* thanks Helon Simões Oliveira, Tobias Rojas, and the other anonymous reviewer(s) for their contribution to the peer review of this work. A peer review file is available.

Reprints and permissions information is available at <http://www.nature.com/reprints>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

© The Author(s) 2026