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Turnover-driven loss of forest-dependent species changes avian species richness, functional diversity, and community composition in Andean forest fragments

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ABSTRACT

Andean forests, a hotspot of biodiversity, have suffered extensive fragmentation, yet we have little understanding of how this process has affected biodiversity. We surveyed bird communities across a gradient of fragment sizes (10–170 ha) and a continuous forest reference site in the Colombian Western Andes. Using a multi-species occupancy model to combine survey data from audio-visual transect surveys, mist netting, and playbacks for owls, we estimated alpha and beta taxonomic and functional diversity. We asked whether (1) habitat amount (patch size), edge effects, or selective logging affect bird occupancy and drive changes to diversity, (2) functional and taxonomic diversity respond similarly to fragmentation, and (3) compositional changes result from species turnover or nested species loss. Species richness declined with decreasing habitat amount, increasing edge density, and increasing disturbance through selective logging. These effects were driven by the loss of forest-dependent species, which were also area sensitive: 30 such species were absent from fragments, even the largest ones (>150 ha). Area-sensitive species were also edge sensitive and increased in occupancy in unlogged forest. We further found high beta diversity (0.78) driven by species turnover (85% of dissimilarity) along the gradient. Despite extensive turnover to non-forest species within functional groups, functional trait richness and dispersion significantly declined with habitat amount. Small fragments may mimic the structure and composition of early-successional Andean forests, driving spatial turnover patterns favoring disturbance-adapted species at the expense of primary-forest specialists. Large forest reserves are therefore required to conserve forest-dependent Andean birds.

1. Introduction

Forest loss is among the most important drivers of biodiversity loss worldwide (Achard et al., 2014; Watson et al., 2016), particularly in the humid tropics (Barlow et al., 2018). Even small amounts of habitat loss in intact forested landscapes can negatively affect vertebrate biodiversity (Betts et al., 2017), and ongoing forest loss in biodiversity hotspots is a leading driver of vertebrate

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extinction risk (Tracewski et al., 2016; Betts et al., 2017). Deforestation may lead to forest fragmentation, where remaining forest is isolated into small patches (Wilson et al., 2016). This fragmentation negatively affects biodiversity, with fewer species encountered in smaller and more isolated patches (Haddad et al., 2015; Fletcher et al., 2018). While some biodiversity can persist in disturbed landscapes, a subset of tropical vertebrate communities is exclusively tied to primary forest (Gibson et al., 2011; Alroy, 2017).

Understanding how fragmentation drives biodiversity loss requires an understanding of its effects at different scales (Bhakti et al., 2018; Vergara et al., 2020). At the patch scale, habitat amount (fragment area) determines how many species persist (Ferraz et al., 2007; Rueda-Hernandez et al., 2015; Ulrich et al., 2016). At the within-patch scale, fragmentation increases ease of human access to tropical forests, leading to additional impacts of disturbance, including selective logging (Barlow et al., 2016; Alroy, 2017). Selective logging of large trees shifts plant community composition and structure towards secondary forest (Aubad et al., 2008) and changes the richness and composition of bird communities (Thiollay, 1997; Burivalova et al., 2014; Arcilla et al., 2015). Finally, fragmentation frequently leads to changes to biotic and abiotic conditions near the edge of forest patches ("edge effects"; Pfeifer et al., 2017), to which bird species may respond positively or negatively (Manu et al., 2007; Banks-Leite et al., 2010). Few studies, however, have concurrently addressed drivers of biodiversity loss at the patch and within-patch scales in a fragmented tropical landscape.

In addition to the question of scale, it is important to understand *how* avian biodiversity is lost in fragments, as species richness trends are often decoupled from species turnover (Hillebrand et al., 2017). Finding nested patterns of species loss, where small habitat patches contain a subset of the species found in large habitat patches (Patterson, 1987), suggests community-level change occurs through gradual, non-random loss of species in fragments. Nested species loss is commonly observed among avifauna in fragmented landscapes (Wethered and Lawes, 2005; Hill et al., 2011; Smith et al., 2018). Alternatively, changes to species composition between assemblages might also reflect species turnover (Baselga, 2010). Generalist and disturbance-adapted species can colonize small fragments, causing changes to species composition independent of species loss (Carrara et al., 2015; Keinath et al., 2017). It is therefore important to understand the contributions of nestedness and turnover when studying fragmented landscapes and how these changes are associated with changes in species traits. Measuring functional diversity (Petchey and Gaston, 2006) allows us to understand if species loss or turnover engenders a loss or gain of functional roles, or 'what organisms do' in the ecosystem, which are key to healthy ecosystem functioning. Understanding changes to biodiversity must account for imperfect detection of species, however, as detectability differs across avian functional groups (Palacio et al., 2020a).

One ecosystem particularly at risk to ongoing forest fragmentation is the montane cloud forest of the Andes, which covers over 300,000 km² stretching from Venezuela to Argentina (Tejedor-Garavito et al., 2012; Hermes et al., 2018; Karger et al., 2021). These forests represent a global hotspot of restricted-range bird species richness (Orme et al., 2005; Karger et al., 2021) and are undergoing high levels of deforestation (Tejedor-Garavito et al., 2012; Tracewski et al., 2016; Karger et al., 2021). In Colombia, for example, only ~30% of originally forested lands above 1500 m remain (Etter et al., 2006), with conversion to agricultural lands and urban expansion driving deforestation (Armenteras et al., 2007, 2011). Andean birds are vulnerable to habitat loss because they occur in narrow altitudinal bands (Graves, 1988), leading to small range sizes and restricting them to specific climatic conditions. Many Andean species are further predicted to suffer climatically driven range declines with climate change (Velásquez-Tibatá et al., 2013). Andean birds respond negatively to fragmentation, with species loss occurring in cloud forest fragments (Renjifo, 1999; Aubad et al., 2010; Palacio et al., 2020b). Other studies have detected negative effects of isolation (Aubad et al., 2010) and edge (Restrepo and Gomez, 1998) effects, suggesting a sensitivity to landscape variables.

Here, we sampled bird diversity along 500-meter transects in mid-to-late successional forest fragments in the Colombian Western Andes, using a multi-species occupancy model to infer species richness, functional diversity, and community composition at each site. We asked three questions about Andean bird communities: (1) Are habitat amount, selective logging, or edge effects more important in driving alpha diversity patterns in fragmented Andean landscapes? (2) Do species richness and functional diversity patterns differ in their response to fragmentation? And (3), is beta diversity in the Andes driven more by nested species loss in fragments or species turnover? If Andean forest-dependent birds show a nested response to fragment size, we would expect to see a gradual loss of species along our gradient. If edge effects or vegetation structure are more important, then species richness should decrease with greater edge density or logging intensity regardless of habitat amount. Alternatively, if turnover to non-forest and disturbance-adapted species drives changes to small-fragment bird communities then we would expect little change to overall species richness and high beta diversity across the gradient. We additionally would predict that functional diversity should decline with smaller habitat amounts, higher edge density, and greater logging as environmental filtering associated with disturbance limits the range of functional traits that can persist. Alternatively, functional diversity could remain unchanged or even increase if species turnover occurs within functional groups or disturbance-adapted birds in fragments occupy distinct areas of functional space from forest-dependent species.

2. Methods

2.1. Study area and sites

We surveyed bird communities in the Serranía de los Paraguas range of the Colombian Western Andes, a Birdlife International important bird area (Birdlife International, 2021) and center of endemism (Ocampo-Peñuela and Pimm, 2014). We sampled primary forest fragments on private lands in the municipality of El Cairo, Valle del Cauca department, in collaboration with a local conservation NGO (Serraniagua; www.serraniagua.org). We selected isolated fragments of primary Andean forest on the east slope of the massif and within the same altitudinal band (1950–2300 m.a.s.l.) to control for altitudinal effects on community composition. This forest type is characterized by humid conditions, numerous epiphytes, and a community of > 200 tree species (Aubad et al., 2008). Forests in our study landscape were heavily fragmented, with ongoing forest clearing for conversion to cattle pasture and smallholder coffee

plantations. To sample a full gradient of fragment sizes, we stratified forest fragments into large (≥ 100 ha), medium (30–50 ha), and small (≤ 20 ha) size categories and selected a minimum of two replicates of each ($N = 8$ fragments, range = 10–173 ha; Table 1); all sites chosen were surrounded by cattle pasture. We also sampled in a continuous forest reference site (RCN Cerro El Inglés), a ~ 750 ha private reserve connected to thousands of hectares of Andean and Chocóan primary forest. Land-use histories, particularly disturbance by selective logging (Aubad et al., 2008), differed substantially within and across sites; we therefore created 500-meter sampling transects ($N = 14$) in forest interior, placed on existing trails. We placed two transects in large-sized fragments: one in a more disturbed site and the other in a less-disturbed forest site.

2.2. Multi-species, multi-survey-type occupancy model

We applied a novel multi-species, occupancy model without data augmentation (Devarajan et al., 2020; hereafter MS-MSOM), implemented in a Bayesian framework, to multi-survey-type presence-absence data. Occupancy models enable us to estimate the probability of a species' true presence at a site from detections across repeated sampling visits (Royle and Kéry, 2007), accounting for imperfect detection. The full model is specified in the Supplemental Materials; briefly, it was formulated as a hierarchical state-space model (Royle and Kéry, 2007) with a state process model of transect-level occupancy described by a Bernoulli distribution and an observation model of repeated detections from each survey technique described by a binomial distribution accounting for differences in sampling effort. We performed audio-visual transect surveys, understory mist netting, and playback surveys for owls across 14 transects at nine sites (Table 1), keeping spatial coverage equal across survey types. We then used an intercept term for each survey type in the detectability sub-model of the MS-MSOM to integrate presence-absence data across these techniques (see Supplemental Materials for details). Thus, each species had a unique detectability for each of four survey methods (Boreal summer and winter mist netting were modeled separately), and species occupancy and detection parameters were assumed to covary. We fitted five fixed-effect covariates on transect-level occupancy: percentage forest cover and edge density (m/ha) within 1 km of the transect, an index of vertical vegetation structure along the transect, and two PCA axes describing the densities of understory vegetation and large-diameter trees, respectively. Methods of predictor variable collection are described in the Supplemental Materials. We also included a random effect of site ($N = 9$) to account for the non-independence of survey transects located within the same forest fragment. All analyses were performed in R (version 3.5.1; R Core Team, 2021); the MS-MSOM model was implemented in Just Another Gibbs Sampler (JAGS) using the *jagsUI* package (Kellner, 2019), with 5000 samples in total. Model goodness-of-fit was assessed for each species using Bayesian p-values (Broms et al., 2016).

2.3. Analysis of alpha diversity

We analyzed alpha diversity using a combination of beta estimates from the MS-MSOM and *post-hoc* analyses performed on the median site-by-species occupancy (z) matrix. For each occupancy covariate in the MS-MSOM, we calculated the cross-species mean and standard deviation of the median beta estimate across the 5000 samples of the posterior distribution. We also determined the number of species whose occupancy was significantly positively or negatively affected by each covariate based on whether the 90% Bayesian credible interval overlapped zero. Overall effect of each predictor variable on each species was inferred from the sign and magnitude of the median beta estimate across all samples. We looked at the same effects on two a priori-defined community subsets: foraging guilds and categories of forest dependence. We sorted all species into forest-dependent (= "forest specialist"), forest

Table 1

Study sites and survey results in forest fragments in El Cairo municipality. Sites correspond to a gradient of fragment sizes sampled in the same landscape in the Western Andes of Colombia, ordered by increasing patch size. Transects correspond to 500-meter sampling transects within the forest; coordinates correspond to the transect center point. Species totals correspond to the total number of species detected using a sample method across all sites, while hours correspond to total time that 12 mist nets were operated or transect surveys conducted at a site. NSR = naïve species richness detected at a site across all survey types. ESR = species richness estimated for the site using the median z matrix of the MS-MSOM.

Site	Latitude	Longitude	Area	Transect	Mist Net		Transect Survey		Owl Survey		NSR	ESR	Δ SR
					Hrs.	Spp.	Hrs.	Spp.	Sur.	Spp.			
1	4° 46.984'	76° 12.511'	10	La Cancana	45.0	44	16.0	44	2	1	66	95	29
2	4° 47.866'	76° 11.744'	14	La Gitana	44.0	36	13.0	48	2	1	69	106	37
3	4° 47.793'	76° 11.286'	28	La Tulia	45.0	34	11.5	37	2	1	60	88	28
4	4° 45.904'	76° 08.260'	37	Las Brisas	54.5	41	15.0	31	3	1	58	77	19
	4° 45.711'	76° 08.101'		El Tigre	53.0	37	12.5	26	2	1	49	74	25
5	4° 46.857'	76° 13.017'	43	Altamira	49.0	39	19.0	55	2	2	78	106	28
	4° 43.700'	76° 14.706'		Altomira	52.0	28	15.0	51	2	2	68	92	24
6	4° 43.474'	76° 15.087'	107	El Eden	49.0	31	18.0	52	3	3	67	100	33
	4° 42.277'	76° 14.630'		El Lagito	51.0	28	10.0	54	2	2	71	112	41
7	4° 42.400'	76° 14.986'	147	La Sonora	50.0	41	15.5	58	3	4	80	116	36
	4° 42.384'	76° 12.930'		La Guardia	50.0	30	21.0	53	2	2	71	93	22
8	4° 41.964'	76° 13.254'	173	El Rocio	47.0	16	14.5	59	2	2	66	81	15
	4° 44.752'	76° 17.448'		El Brillante	53.0	44	19.0	72	3	2	93	131	38
RNC El Ingles	4° 44.526'	76° 17.655'	~ 750	El Ingles	54.0	48	18.0	74	2	2	100	137	37
						696.5	124	218.0	135	32	4	178	

generalist, and non-forest (or “forest visitor”) categories based on the criteria in Bennun et al. (1996) and using the habitat preferences in del Hoyo et al. (2020); see Table S6 for all species categorizations. Forest-dependent species were defined as only occurring in the interior of primary forest, while forest generalists were species commonly encountered in disturbed forest habitat such as treefall gaps, forest edge, secondary forest, or agroforests. Foraging guilds were assigned based on the primary diet item for a species (see Table S6); if two or more diet items were commonly exploited, the species was classified as an omnivore. We used principal components analysis (PCA) to ordinate the five covariate median beta estimates for each species and plotted the first two axes to visualize correlations among species responses to each covariate. Changes to estimated alpha richness were visualized by plotting the transect-level richness

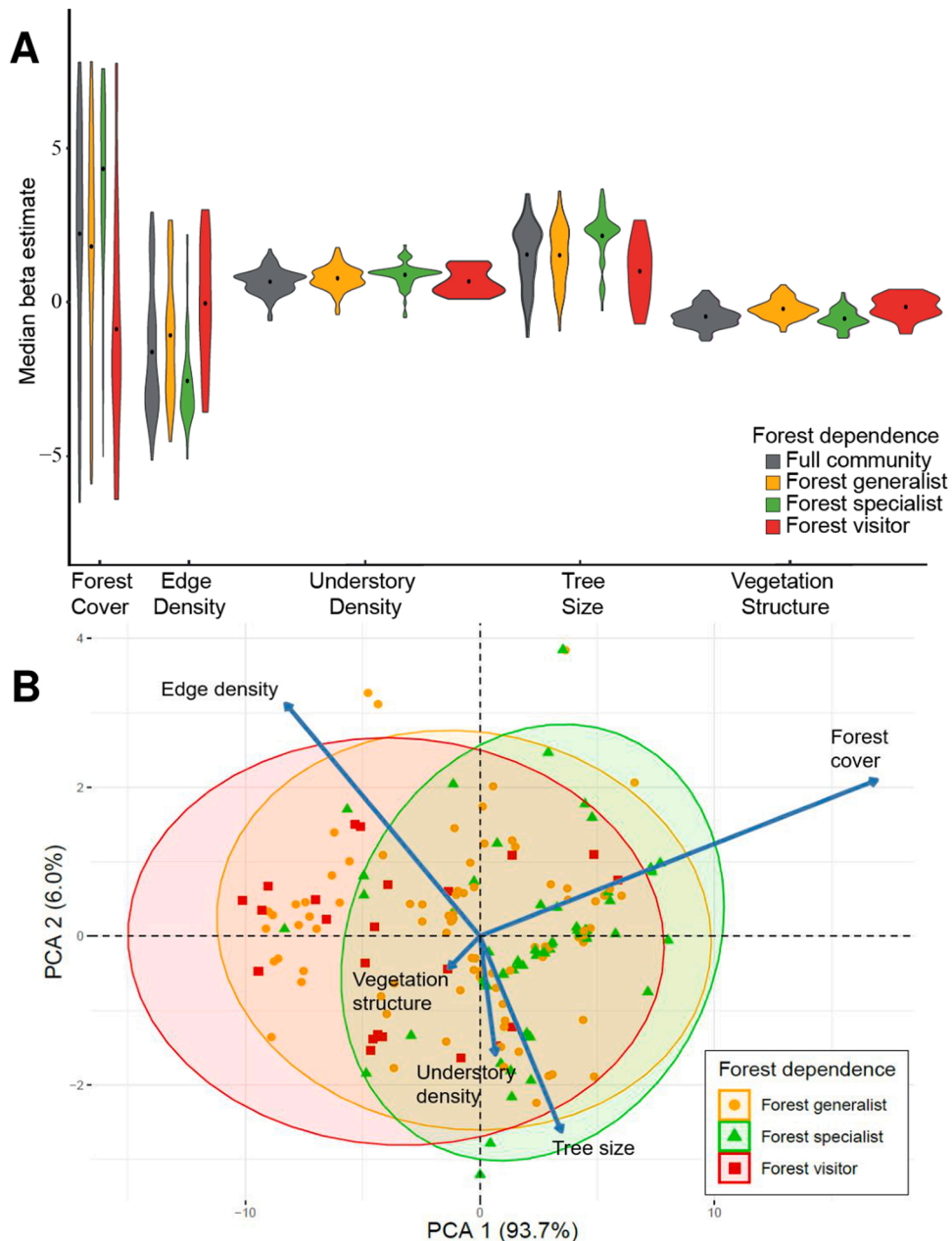


Fig. 1. Effect of fragmentation covariates on the occupancy of Andean birds. (A) The full community did not respond strongly to fragmentation variables (grey). However, both forest specialist species (forest-dependent habitat specialists; green) and forest visitors (species with non-forest habitat preferences; red) responded strongly and in contrasting ways to percentage forest cover (a proxy for habitat amount), edge density, and density of large-diameter trees. Violin plots show the median beta estimates for all species in the community subset and black dots represent mean values. Values of beta estimates are provided in Table S2. (B) PCA showing associations between median beta estimates across species; responses to forest cover and edge density were inversely correlated.

from the median z matrix against percentage forest cover.

For functional alpha diversity, we calculated standardized effect sizes of two functional diversity metrics (FD and mean nearest taxon distance; see [Supplemental Materials](#)) using the median z matrix derived from the MS-MSOM. We then fitted single-predictor linear mixed models ([Harrison et al., 2018](#)) to assess the effects of five covariates included in the MS-MSOM on functional diversity, and included a random effect of site (to control for the non-independence of transects in the same fragment); we ran models using the *lme4* package ([Bates et al., 2015](#)). We did not run a multiple regression because sample sizes were too low (i.e., $n/k < 10$; [Harrison et al., 2018](#)). We ranked all candidate models and the null model (random intercept of site only) using the Akaike Information Criterion for small sample sizes (AIC_c; [Burnham and Anderson, 2002](#)) and considered models equivalent to the best model if they were within 2 Δ AIC_c. In addition, we visualized changes to species composition across sites using non-metric multidimensional scaling (NMDS; [Kruskal, 1964](#)). The NMDS was run in the *metaMDS* function of the *vegan* package ([Oksanen et al., 2019](#)) using the Jaccard similarity index to quantify differences between assemblies. We plotted 95% ellipses around assemblies representing continuous forest and large, medium, and small fragments using the *ordihull* function of the same package. To test for significant differences in species composition, we then ran a permutational multiple analysis of variance with 1000 permutations (PERMANOVA; [Anderson, 2001](#)) on the median z matrix, using four fragment size categories (continuous forest, and large, medium, and small fragments) as the response variable.

2.4. Beta diversity partitioning of taxonomic and functional diversity

We calculated overall taxonomic and functional beta diversity using the median site-by-species z matrix. For taxonomic beta diversity, we calculated three values using the Jaccard dissimilarity index: the overall dissimilarity (β_{JAC}) and dissimilarity subsets partitioned into species turnover (β_{JTU}) and nestedness components (β_{JNE} ; [Baselga, 2010](#)). We used the Baselga dissimilarity indices because we were specifically interested in beta diversity driven by nestedness ([Legendre, 2014](#)). We calculated values for the full community and our foraging guild and forest dependence community subsets. For the functional beta diversity analysis, we also used the FD measure of functional diversity ([Petchey and Gaston, 2002](#)), the sum of the branch lengths of a functional dendrogram. We built a functional dendrogram from our functional trait matrix by creating a Gower dissimilarity matrix ([Gower, 1971](#)) of all species pairs and then using the UPGMA clustering method. We then partitioned beta diversity according to [Leprieur et al. \(2012\)](#) extension of the Baselga model using the Jaccard dissimilarity index, similarly yielding overall functional dissimilarity (β_{JAC}), a nestedness component (β_{JNE}), and a turnover component (β_{JTU}). We did not use a multidimensional trait space partitioning method (e.g., [Villéger et al., 2013](#)) due to the large number of traits and species. We calculated taxonomic beta diversity metrics using the *beta.multi* function of the *betapart* package ([Baselga and Orme, 2012](#)). Functional beta diversity metrics were calculated using the *phylo.beta.multi* function of the same package.

3. Results

3.1. Avifaunal surveys and model fit

Across 89 days of field sampling on our 14 transects, we detected 178 bird species across all sample methodologies, encompassing 35 families and 141 genera ([Table S5](#)). The most common families were Tyrannidae, Thraupidae, Trochilidae, and Furnariidae. We captured 125 species in mist nets (98 and 100 species during Boreal summer and winter, respectively) over 8350 net hours (12 nets open for 696.5 h) on 80 sampling days. We also detected 135 species on transect surveys over 218 h on 39 sampling days and detected 4 owl species during our 32 playback owl surveys ([Table 1](#)). On transect surveys, we detected 78 species (44% of total species) participating in mixed-species flocks at least once and 68% of 1331 species detections (i.e., detection of a species on a transect on one sampling day) were in mixed-species flocks. The MS-MSOM converged to stable posterior distributions both visually and according to the potential scale reduction statistic (Gelman-Rubin Diagnostic) value of $\hat{R} < 1.1$ and was well specified for all species according to the Bayesian p-values (all p-values > 0.05 ; [Table S6](#)). On average, the estimated species richness at a site added 29.4 ± 7.9 (mean \pm standard deviation) species to the observed richness value, while occupancy for each species increased by 2.3 ± 2.8 (mean \pm standard deviation) sites.

3.2. Species-specific occupancy patterns

Occupancy across the Andean bird community increased with increasing forest cover within 1 km, our proxy for habitat amount (mean of median β estimates = 2.22; [Fig. 1a](#)). We also found an overall trend of decreasing occupancy with increasing edge density (mean of β estimates = -1.62) and increasing occupancy with greater densities of large-diameter trees (mean of β estimates = 1.54); see [Table S6](#) for species-specific median beta estimates. Overall, 55 species showed significant responses to percentage forest cover (42 positive, 13 negative) while 42 species were significantly edge sensitive (all negative responses) and 37 species had significant positive responses to higher large-diameter tree densities ([Table S2, Fig. S1](#)). Mean beta estimates for vegetation structure and understory density were near zero, with few significant effects on occupancy. However, fragmentation effects differed significantly between community subsets. Forest-dependent species showed a positive response to percentage forest within 1 km (mean of β estimates = 4.16, [Fig. 1a](#); 29 significantly positive responses) and increasing large-tree density (mean of β estimates = 2.01; 25 significant positive responses), and a negative response to edge density (mean of β estimates = -2.63; 27 significant negative responses). Non-forest species, on the other hand, showed the opposite trend of increasing occupancy with declining percentage of forest and increasing

edge density (Fig. 1a). Forest-generalist species had intermediate β estimates for all covariates (Table S2). Diet guilds also differed in their response to fragmentation: carnivore and insectivore occupancy increased with greater percentages of forest cover and lower edge densities, whereas granivores showed the opposite pattern (Table S2, Fig. 2b).

Species responses to three of five covariates were correlated (Fig. 1b). Area-sensitive species also showed negative responses to increasing edge density (Pearson's $r = -0.88, p < 0.001$) and positive responses to higher densities of large-diameter trees ($r = 0.71, p < 0.001$), while late-successional species (preferring large-diameter trees) had a greater edge aversion ($r = -0.95, p < 0.001$). The first PC axis explained 94% of variance and had high loadings for percentage forest cover (0.88) and edge density (-0.43); Eigenvalues and axis loadings are available in Tables S3 and S4. Response to understory vegetation density and vegetation structure were uncorrelated with other covariates. The species groups showing significant area-sensitivity included forest-dependent Tyrannid flycatchers (*Leptopogon rufipectus*, *Myiophobus flavicans*, *Phyllomyias cinereiceps*, *Pseudotriccus pelzelni*), mid-story and understory-foraging insectivores (*Cyphorhinus thoracicus*, *Dendrocincla tyrannina*, *Premnomis guttuliger*, *Thripadectes ignobilis*, *Xiphorhynchus triangularis*), large-bodied frugivores (*Pharomachus auriceps*, *Pipreola riefferii*, *Snowornis cryptolophus*, *Turdus serranus*), forest owls (*Glaucidium nubicola*, *Megascops ingens*), and many Colombia-endemic species (*Chlorochrysa nitidissima*, *Cyanolyca pulchra*, *Iridosornis porphyrocephalus*, *Habia cristata*). By contrast, species with higher occupancy in small fragments included edge-adapted generalists (*Eubucco bourcierii*, *Tangara gyrola*, *Turdus ignobilis*, *Zimmerius chrysops*), secondary-growth-adapted hummingbirds (*Uranomitra franciae*, *Sauceottia saucerrottei*, *Chlorostilbon melanorynchus*, *Colibri delphinae*), and some boreal migrants (*Catharus ustulatus*, *Piranga rubra*).

3.3. Alpha taxonomic and functional diversity

Detection-corrected estimates of species richness declined with decreasing percentage forest cover (Fig. 2a), and this loss was most pronounced between the continuous forest reference site and large fragments. Roughly thirty forest-specialist species only occurred in continuous forest and estimated insectivore and carnivore richness also declined with decreasing forest cover (Fig. 2b). Our analysis of functional diversity (Table 2) found strong support for an effect of habitat amount on both overall functional trait diversity and trait dispersion- in both cases there was a greater than 90% chance this was the best model. After controlling for species richness, both overall functional trait diversity (SES FD: $\beta = 0.025, \chi^2 = 9.53, p = 0.002, \Delta AIC_c$ to null model = 5.48; Fig. 2d) and the dispersion of functional traits (SES meanNTD; $\beta = 0.036, \chi^2 = 15.34, p < 0.001, \Delta AIC_c$ to null model = 11.30) significantly declined with declining habitat amount, and small-fragment bird assemblages were underdispersed. MeanNTD also significantly increased with large-tree

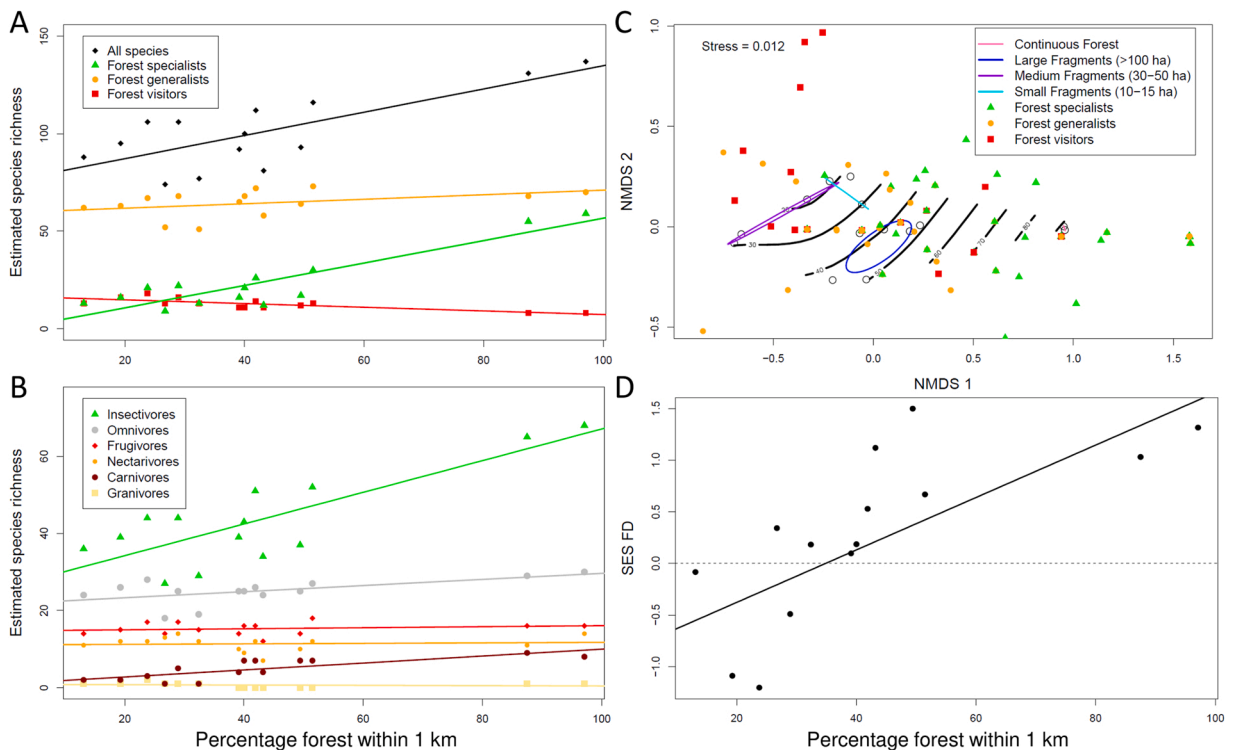


Fig. 2. Changes to taxonomic diversity, functional diversity, and community composition. Both forest dependent species (A) and insectivore and carnivore richness (B) declined with declining percentage of forest within 1 km, a proxy for habitat amount. Species richness numbers are detection-corrected estimates from the median z matrix of the MS-MSOM. (C) Extensive species turnover occurred from continuous forest to even large (> 100 ha) fragments. Small and medium-sized fragments showed similar species composition. (D) Functional diversity declined with habitat amount, with underdispersed assemblages in small fragments.

Table 2

AICc tables of mixed models of fragmentation effects on alpha functional diversity. The response variable was the standardized effect size (SES) of two functional diversity metrics. Marginal r^2 corresponds to the goodness-of-fit of just the fixed effects, while conditional r^2 corresponds to the overall goodness-of-fit of the model. Bolded predictor variables indicate a significant statistical effect. P-values indicate whether a model was significantly better than the null model according to a likelihood ratio test.

SES FD								
Variable	β	Mar. r^2	Cond. r^2	Df	log L	ΔAIC_c	w_i	p
Percentage forest cover	0.025	0.52	0.98	4	-6.32	0.00	0.90	0.002
Null model		0.00	0.96	3	-11.08	5.48	0.06	
Tree size	0.087	0.02	0.97	4	-10.51	8.38	0.01	0.28
Edge density	-0.013	0.01	0.96	4	-10.86	9.10	0.01	0.51
Vegetation structure	-0.064	0.00	0.96	4	-10.89	9.16	0.01	0.54
Understory density	0.039	0.00	0.96	4	-10.97	9.32	0.01	0.64
SES MeanNTD								
Variable	β	Mar. r^2	Cond. r^2	Df	log L	ΔAIC_c	w_i	p
Percentage forest cover	0.036	0.66	0.99	4	-6.33	0.00	0.99	< 0.001
Tree size	0.199	0.05	0.99	4	-11.74	10.82	0.00	0.03
Null model		0.00	0.95	3	-14.00	11.30	0.00	
Understory density	0.153	0.05	0.97	4	-12.90	13.14	0.00	0.14
Vegetation structure	-0.099	0.01	0.95	4	-13.74	14.82	0.00	0.47
Edge density	-0.011	0.01	0.95	4	-13.9	15.15	0.00	0.66

density ($\beta = 0.199$, $\chi^2 = 4.52$, $p = 0.03$), though this model was not within 2 ΔAIC_c of the best model.

3.4. Beta taxonomic and functional diversity

We found high taxonomic beta diversity across our gradient of habitat amount (0.79), of which 85% was explained by species turnover (Table 3). The nestedness beta diversity component was high for carnivores (60%), and slightly greater for forest-dependent species (29%) and insectivores (23%), yet for most diet guilds and all forest dependence categories at least two thirds of overall beta diversity was explained by species turnover. In particular, frugivores and nectarivores showed the highest proportion of beta diversity due to turnover (~90%). Species composition therefore changed with habitat amount, with the greater similarity in composition occurring between sites with similar percentages of forest cover (Fig. 2c). There was no overlap in the 95% ellipses of large (>100 ha) fragments and continuous forest, while small and medium fragments differed from large fragments but showed overlap in composition; the NMDS accurately captured community composition (stress = 0.01). Furthermore, the PERMANOVA revealed significant differences in composition across fragment size categories (Df = 3, $F = 10.16$, $p < 0.001$, $r^2 = 0.75$). Functional diversity patterns closely matched taxonomic diversity- we found high overall beta diversity (0.68), which was primarily (74%) explained by functional turnover rather than loss of functional diversity (26%; Table 3). Turnover of branch tips within clusters of the functional dendrogram (functional groups) therefore explained more dissimilarity than loss of overall branch length (Fig. 3).

4. Discussion

We found that Andean bird communities are sensitive to declining habitat amount, increasing edge density, and selective logging. Fragmentation effects on Andean birds were generated by two simultaneous mechanisms. First, forest-dependent species richness declined with fragment size and many species were lost from even large (>100 ha) fragments. These species were both edge- and area-

Table 3

Beta diversity partitioning of taxonomic and functional diversity. Sample sizes refer to the number of species included in each community subset. Overall beta diversity is calculated across all sites ($N = 14$ transects). Partitioned diversity represents the proportion of beta diversity attributable to nested species loss (β_{JNE}) and species turnover (β_{JTU}) across the fragment size gradient.

Grouping	N	β_{JAC}	β_{JTU} (turnover)	Prop. β_{JTU}	β_{JNE} (nestedness)	Prop. β_{JNE}
Full community	178	0.78	0.67	0.85	0.12	0.15
<i>Forest Dependence</i>						
Forest specialist	64	0.87	0.62	0.71	0.23	0.29
Forest generalist	91	0.71	0.61	0.86	0.10	0.14
Forest visitor	23	0.82	0.73	0.89	0.09	0.11
<i>Diet Guilds</i>						
Insectivores	81	0.80	0.61	0.76	0.19	0.24
Frugivores	24	0.75	0.68	0.91	0.07	0.09
Nectarivores	23	0.83	0.78	0.94	0.05	0.06
Carnivores	9	0.85	0.34	0.40	0.51	0.60
Omnivores	38	0.72	0.59	0.83	0.12	0.17
<i>Functional Diversity</i>						
Full community	178	0.68	0.50	0.74	0.18	0.26

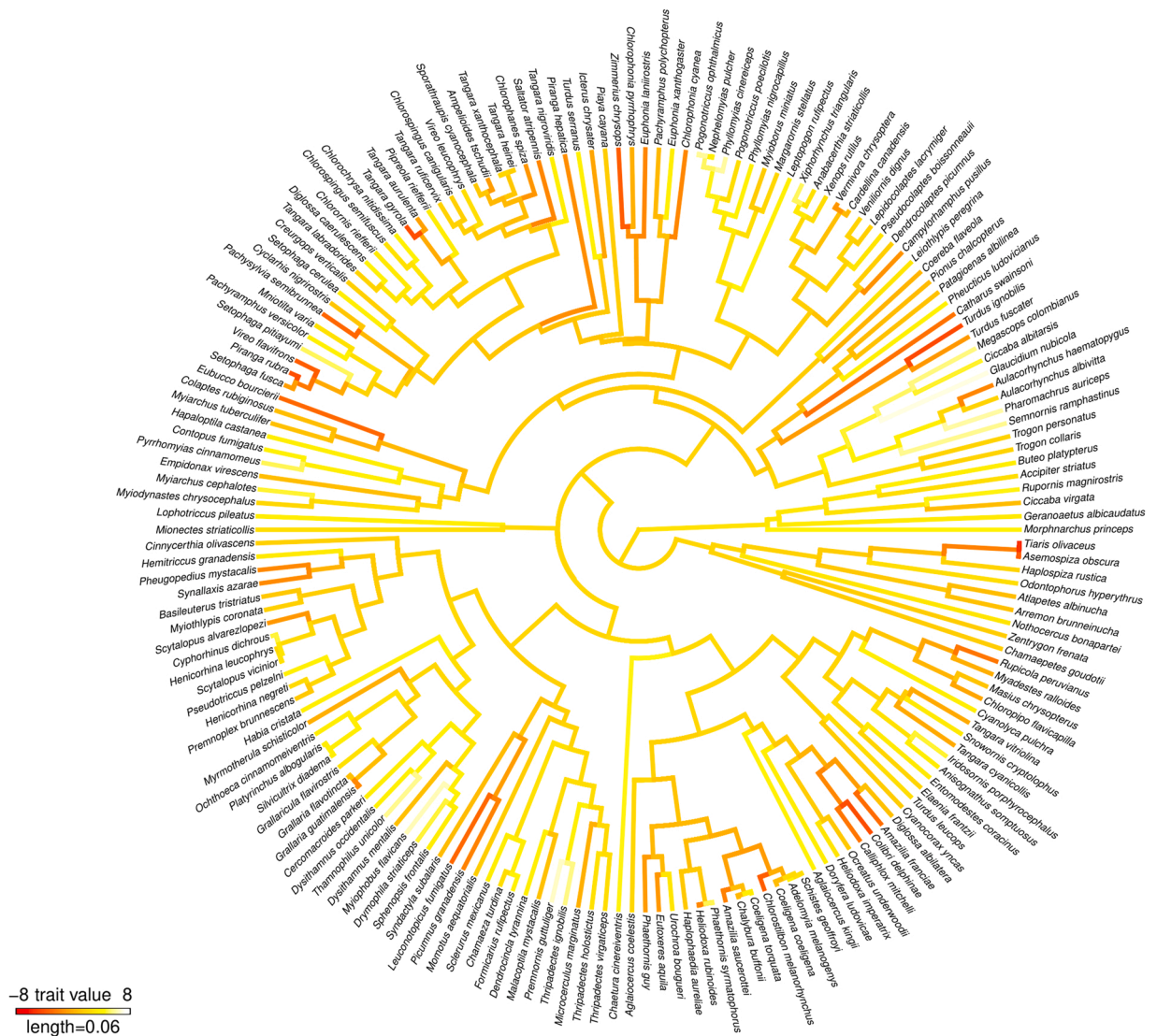


Fig. 3. Median beta estimates of species responses to percentage forest cover mapped onto a functional dendrogram. Each cluster represents a functional grouping constructed using pairwise Gower dissimilarity values from a functional trait table. Bright red colors indicate species that increased in occupancy in small fragments, while species with light yellow branch tips increased in occupancy with increasing habitat amount. Many functional clusters contain both area-sensitive and area-insensitive species, resulting in high functional turnover (~74%) across the habitat amount gradient. Other functional groups such as forest flycatchers (top right), forest owls and raptors (right) and understory insectivores (bottom left) showed a more uniform area-sensitivity and were lost from small fragments.

sensitive and associated with unlogged primary forest (Fig. 1a,b). Second, we found extensive species turnover to non-forest and generalist species occurring in association with declining habitat amount. Community composition in fragments was dominated by forest-generalist and non-forest species (Fig. 2c) that may be adapted to natural early-successional and disturbed habitat (e.g., treefall gaps, landslides). Whereas insectivores and carnivores declined with decreasing habitat amount, nectarivores and frugivores showed no change to species richness (Fig. 2b) but underwent high (~90% of dissimilarity; Table 3) compositional turnover. Species richness was therefore a poor indicator of community composition of Andean fragment communities, as elsewhere in the tropics (Cazalis et al., 2020). Overall functional diversity and the degree of dispersion of functional traits declined significantly with habitat amount (Fig. 2d), but turnover within functional groups also occurred simultaneously with taxonomic turnover (Fig. 3).

4.1. Negative habitat amount and edge effects on forest-specialist species

Declining habitat amount and increasing edge density led to declines of forest-dependent species, but not forest-generalist or non-forest species. Large fragments lost ~30 species of forest-dependent birds relative to continuous forest, and 42 species showed a

significant association with increasing habitat amount. Our results therefore support Gibson et al. (2011) finding that a portion of tropical forest biodiversity can only be conserved in undisturbed primary forest. Forest-dependent species show greater sensitivity to fragmentation (Morante et al., 2015; Khimoun et al., 2016), and work in Ecuador also found that a subset of cloud-forest birds had strong preferences for primary forest (Becker et al., 2008). While our study was conducted at a small number of sites, species extirpations in fragments matched those in a study in the Colombian Central Andes (Cataño-Villa and Patiño-Zabala, 2008). Our results furthermore echo other Andean studies showing that a subset of species is sensitive to forest loss (Aubad et al., 2010; Cazalis et al., 2020) and edge effects (Restrepo and Gomez, 1998), and that specific functional groups are lost from fragments (Palacio et al., 2020b). Like Carrara et al. (2015) and Cerezo et al. (2010), we found that proportion of forest within 1 km was the primary driver of species presence in fragments. However, area-sensitivity in forest-dependent birds was highly correlated with edge-sensitivity, providing further support for the idea that edge effects, and therefore habitat configuration, may drive negative species responses to declining habitat amount (Banks-Leite et al., 2010), particularly for cloud-forest birds (Martínez-Morales, 2005; Jankowski et al., 2021).

Loss of forest-dependent species may be especially pronounced in our study landscape because the primary matrix type was less-permeable cattle pasture, which can increase the negative effects of isolation (Boesing et al., 2018) and forest edge (Hatfield et al., 2019) compared to more permeable matrix types such as tree plantations (Renjifo, 2001; Nogueira et al., 2021). Forest-dependent species may persist better in landscapes with more permeable matrices, though land clearing for cattle pasture is predicted to be the main driver of Andean forest loss by 2050 (Rodríguez-Eraso et al., 2013). Furthermore, conversations with landowners suggest that our study landscape was fragmented ~50–60 years prior to sampling, such that much of the ‘extinction debt’ (Kuussaari et al., 2009) of forest-dependent species loss may have been paid. In addition to these factors, forest-dependent species may be outcompeted in fragments by species pre-adapted to fragmentation (see Section 4.2). Concerningly, many forest-dependent species currently categorized by the IUCN and Colombian authorities as only Least Concern (e.g., *Premnornis guttuliger*, *Myiophobus flavicans*, *Pharomachrus auriceps*) were significantly area-sensitive and required forest fragments of more than 100 ha. Many IUCN-listed species endemic to the Colombian Andes were also significantly area-sensitive, such as *Chlorochrysa nitidissima* (Near Threatened), *Glaucidium nubicola* (Vulnerable), and *Iridosornis porphyrocephalus* (Near Threatened). Accounting for remaining habitat and minimum habitat area requirements in determining conservation statuses (e.g., Tracewski et al., 2016; Brooks et al., 2019) should therefore be a priority for Andean forest birds.

4.2. Functional diversity loss despite functional and taxonomic turnover

We found high species turnover, ~80% of all taxonomic and functional dissimilarity, along our fragment size gradient; our findings echo the extensive species turnover documented in Andean fragments and secondary forest (Renjifo, 1999; O’Dea and Whittaker, 2007). Selectively logged fragments and their associated edge effects may mimic the structure and plant composition of naturally occurring disturbed (early successional) plant communities (Tabarelli et al., 2008), such as those caused by landslides (Hilty, 1997; Ohl and Bussmann, 2004), allowing species pre-adapted to disturbance to persist in forest fragments. Andean bird community composition has been shown to be affected by vegetation structure (Jankowski et al., 2013) and forest succession (O’Dea and Whittaker, 2007; Rosselli et al., 2017). We found the highest turnover in nectarivores and frugivores, species most strongly tied to plant community composition, matching the Jankowski et al. (2013) finding of high turnover of these species with tree community composition in the Andes. Tinoco et al. (2017) also found that functional diversity of Andean hummingbirds, but not taxonomic diversity, declined with human disturbance. Despite the relatively small contribution (26%) of functional diversity loss to overall functional dissimilarity, we observed a steep loss of functional diversity with declining habitat amount. While avian functional diversity generally declines with forest fragmentation (Matuoka et al., 2020a), it does not do so evenly. Forest-dependent species can suffer a decline in functional diversity while non-forest species functional diversity increases (Matuoka et al., 2020b), partially offsetting functional diversity loss through functional turnover. However, lost forest-dependent functional guilds may contribute disproportionately to ecosystem functioning (e.g., large-bodied frugivores; Vidal et al., 2019).

4.3. Negative effects of selective logging

Forest-dependent species showed sensitivity to disturbance by selective logging, with occupancy increasing significantly with the density of large-diameter trees (Fig. 1a) for 37 species (Tables S2, S6). Such trees are removed during selective logging (Aubad et al., 2008), and Andean bird communities in Bolivia also showed compositional changes after small-scale vegetation disturbance (Montaño-Centellas and Garitano-Zavala, 2015). In Colombia, bird species richness declined with increasing ease of human access (Aubad et al., 2010), a proxy for disturbance. Generally, our results agree with a large body of literature suggesting that selective logging practices negatively affect forest specialists and change bird community composition (Politi et al., 2012; Arcilla et al., 2015; Burivalova et al., 2015). Vegetation structure is simplified in selectively logged forests, with changes to canopy cover, tree density, and understory vegetation density (Thiollay, 1997; Sekerçioğlu, 2002) and a loss of late-successional tree species (Aubad et al., 2008). Such changes may lead to the loss of specialized foraging microhabitats (Stratford and Stouffer, 2015) and breeding substrates (Politi et al., 2010), or a reduction in insect prey density (Vergara et al., 2020). Our study may, in fact, underestimate effects of logging, because vegetation structure affects tropical bird occupancy at scales smaller than our 500-m sampling transects (Bhakti et al., 2018; Vergara et al., 2020).

4.4. Conservation implications: large reserves matter

Thirty species of forest-dependent birds were lost from continuous forest to 100–170 ha fragments, with further declines in smaller

fragments. Similarly, overall avian functional diversity decreased in medium and small fragments. Managers should therefore aim to conserve intact Andean landscapes and increase connectivity of fragments. Area-sensitive species were also sensitive to edge effects and associated with primary forest. Thus, landscape configuration and core area of existing reserves are important considerations in maintaining forest-specialist birds, as elsewhere in the Neotropics (Nogueira et al., 2021), because edge-dominated Andean landscapes contain primarily edge-adapted, early successional, and non-forest species. Furthermore, selective logging, even within large forest tracts, degrades habitat for forest-dependent species, leading to species turnover. Efforts should therefore be made to minimize this practice in primary forest. Compositional change occurred through species turnover rather than nested species loss, suggesting non-gradual species loss in fragments; overall species richness is therefore a poor surrogate for forest-dependent species richness. Because even large fragments contained few forest-dependent species, the most area-sensitive Andean birds can only be conserved in large tracts of primary forest. Our results therefore support the conclusion of Cazalis et al. (2020) that forest-dependent Andean birds are best conserved in large, protected areas that guard against both forest loss and human disturbance.

Ethics statement

Animal capture and manipulation was conducted in full compliance with the Institutional Animal Care and Use Committee of the University of Florida (permit #201709853). Research in Colombia was approved by and conducted under the research permit of the Universidad del Valle (permit #1070). Permission to work in forest fragments was obtained from private landowners prior to visiting each site.

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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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Data archiving statement

R code for all analyses and raw data on bird occupancy will be archived in the Dryad public repository upon acceptance of the manuscript.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01922](https://doi.org/10.1016/j.gecco.2021.e01922).

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