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Ausprey Ian (Orcid ID: 0000-0002-7127-2746)

Functional Response Traits and Altered Ecological Niches Drive the Disassembly of Cloud Forest Bird Communities in Tropical Montane Countrysides

lan J. Ausprey^{1,2,3}, Felicity L. Newell¹, and Scott K. Robinson¹

¹Florida Museum of Natural History and Department of Biology, University of Florida, Gainesville, FL, 32611, USA

² Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern, CH-3012, Switzerland

³Email: iausprey@ufl.edu

ABSTRACT

- 1. Anthropogenic disturbance contributes to global change by reshaping the ecological niche space available to biological communities. Quantifying the range of functional response traits required for species persistence is central towards understanding the mechanisms underlying community disassembly in disturbed landscapes.
- 2. We used intensive field surveys of cloud forest bird communities across seven replicate landscapes undergoing agricultural conversion in the Peruvian Andes to examine how a suite of 16 functional response traits related to morphology, diet, foraging behavior, and environmental niche breadth predict (1) species-specific abundance changes in countryside habitats compared to forest and (2) differential changes to the ecological niche space occupied by communities.
- 3. Our analyses relied on (1) hierarchical distance sampling models to examine the functional predictors of abundance change across the agricultural land use gradient while accounting for imperfect detection and (2) n-dimensional hypervolumes to quantify the expansion and contraction of ecological niche space in countryside habitats.
- 4. Key traits related to increased abundance in early successional and mixedintensity agricultural areas included (1) morphological adaptations to dense understory habitats, (2) plant-based diets (flowers, fruit, and seeds), and (3) broad elevational range limits and habitat breadth. Species occupying mixed and highintensity agricultural land use regimes had mean elevational range limits 20-60% wider than species found within forests. Collectively, ecological niche space expanded within agricultural habitats for traits related to diet and environmental niche breadth, while contracting for foraging and dispersal traits. Such changes were driven by species with unique functional trait combinations.
- 5. Our results reveal the dynamic changes to ecological niche space that underly community structure in disturbed landscapes and highlight how increased niche breadth can ameliorate disturbance sensitivity for generalist species. We emphasize that functional traits can be used to predict changes in community

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structure across disturbance gradients, allowing insights into specific mechanisms underlying community disassembly beyond emergent patterns of functional diversity. By identifying key functional trait groups that align with different countryside habitats, we demonstrate how conservation practitioners can contribute to the retention of avian functional diversity in agricultural landscapes throughout the world.

KEYWORDS

agriculture, bird, countrysides, ecological niche space, functional traits, land-use change

ABSTRACT (Español)

- 1. La perturbación antropogénica contribuye al cambio global al remodelar el espacio de nicho ecológico disponible para las comunidades biológicas. Cuantificar la gama de rasgos de respuesta funcional requeridos para la persistencia de las especies es fundamental para comprender los mecanismos que subyacen al desensamble de la comunidad en los paisajes perturbados.
- 2. Utilizamos muestreos de campo intensivos de las comunidades de aves del bosque nublado en siete paisajes replicados convertidos a uso agrícola en los Andes peruanos para examinar cómo un conjunto de 16 rasgos de respuesta funcional relacionados con la morfología, dieta, comportamiento de forrajeo, y la amplitud del nicho ambiental predicen (1) cambios en las abundancias de especies específicas en paisajes agrícolas ("countrysides") en comparación con el bosque y (2) cambios diferenciales en el espacio del nicho ecológico ocupado por las comunidades.
- 3. Nuestros análisis se basaron en (1) modelos jerárquicos de muestreo por la distancia para examinar los predictores funcionales del cambio de abundancia a través del gradiente de uso de suelo para agricultura teniendo en cuenta la detección imperfecta, y (2) "n-dimensional hypervolumes" para cuantificar la expansión y contracción del espacio de nicho ecológico en los hábitats agrícolas.
- 4. Los rasgos clave relacionados con el aumento de la abundancia en áreas agrícolas de sucesión temprana y de intensidad mixta incluyeron (1) adaptaciones morfológicas a hábitats de sotobosque denso, (2) dietas basadas en plantas (flores, frutas y semillas), y (3) amplios límites de rango de elevación y amplitud de hábitat. Las especies que ocupan regímenes de suelo agrícola mixto y de alta intensidad tenían límites de rango de elevación promedio 20-60 % más amplios que las especies que se encuentran en los bosques. En conjunto, el espacio del nicho ecológico se expandió dentro de los hábitats agrícolas para los rasgos relacionadas con la dieta y la amplitud del nicho ambiental, mientras que se contrajo para los rasgos de forrajeo y dispersión. Dichos cambios fueron impulsados por especies con combinaciones de rasgos funcionales únicos.
- 5. Nuestros resultados revelan los cambios dinámicos en el espacio del nicho ecológico que subyacen a la estructura de la comunidad en los paisajes perturbados y destacan cómo una mayor amplitud del nicho puede mejorar la sensibilidad a las perturbaciones para las especies generalistas. Enfatizamos que los rasgos funcionales pueden utilizarse para predecir los cambios en la estructura de la comunidad a través de gradientes de perturbación, lo que permite comprender los mecanismos específicos que subyacen al desensamble de la comunidad más allá de los patrones emergentes de diversidad funcional. Al identificar grupos de rasgos funcionales claves que se alinean con diferentes hábitats agrícolas como en "countrysides" demostramos cómo los profesionales de la conservación pueden contribuir a la retención de la diversidad funcional de las aves en los paisajes agrícolas en todo el mundo.

Habitat loss and fragmentation within agricultural landscapes alter environmental gradients and the resources required for the persistence of biological communities (Curtis et al., 2018). While the pervasive loss of biodiversity due to Anthropogenetic disturbance has been exhaustively documented throughout the world, less understood are the ecological processes underlying community disassembly (Okie & Brown, 2009). In particular the identification of functional traits that drive the expansion and contraction of ecological niche space following anthropogenic disturbance can provide mechanistic explanations for subsequent changes in community composition (Ausprey et al., 2021; Moore et al., 2008).

The ecological niche occupied by a given community is defined by the cumulative outcome of environmental factors that filter for compatible traits ("fundamental niche") and biotic interactions that restrict species persistence ("realized niche") (Chase & Leibold, 2011; Hutchinson, 1957). Communities disassemble when disturbance alters environmental conditions and biotic interactions to exact non-random species losses, producing novel species assemblages (Zavaleta et al., 2009). While teasing apart the relative contribution of environmental filtering vs. biotic interactions is difficult (Cadotte & Tucker, 2017), the cumulative effect of both processes can be quantified as the expansion or contraction of ecological niche space occupied by communities post-disturbance.

Given the "n-dimensional" nature of ecological niche space (i.e., Hutchinson's "ndimensional hypervolume"), disturbance-mediated changes to the identity and magnitude of niche axes can be defined by species-specific functional traits, or the suite of morphological, physiological and life history characteristics that allow a species to persist or function within specific environmental conditions (Hutchinson, 1957; Petchey & Gaston, 2006). In particular, the correlation between morphology and ecology ("ecomorphology") is widely documented, and morphological traits often predict foraging behavior, diet, habitat preference, and position within ecological networks (Dehling et al., 2016; Pigot et al., 2020; Ricklefs & Travis, 1980). Because functional traits implicitly reflect the range of environmental conditions required for survival, they provide indirect measures of ecological niche axes for a given species or community (Kearney et al., 2010; Pigot et al., 2016). Furthermore, the total ecological niche space occupied by a community of species as defined by their functional traits is similar to the idea of "functional diversity" widely used to quantify biodiversity change in anthropogenic landscapes.

Trait-based analyses of biodiversity response to anthropogenic disturbance are prolific and recent global analyses have pointed towards widespread loss of functional diversity across thousands of species and multiple taxonomic groups in agricultural and other highly disturbed landscapes (Etard et al., 2022; Flynn et al., 2009; Matuoka et al., 2020). In many situations, biotic communities are more functionally depauperate than expected by species richness, suggesting that anthropogenic disturbance poses environmental filters exacting nonrandom species loss (Kraft & Ackerly, 2010). Tropical communities appear particularly sensitive to agricultural disturbance, with larger reductions in functional diversity compared to temperate regions (Etard et al., 2022; Matuoka et al., 2020). However, the simultaneous emergence of increased functional

diversity at some sites indicates the potential for disturbance to also generate novel dimensions of ecological niche space (Etard et al., 2022).

While functional traits are commonly used to quantify functional diversity as an emergent response to environmental gradients across space and time (Jarzyna et al., 2021; Jarzyna & Jetz, 2016), they also provide a predictive method for establishing the mechanistic processes underlying community disassembly (Newbold et al., 2013; Nowakowski et al., 2017; Quesnelle et al., 2014; Socolar & Wilcove, 2019; Todd et al., 2017). Such "functional response traits" describe species-specific responses to anthropogenic disturbance (Hooper et al., 2005; Newbold et al., 2014), yet are rarely used to predict changes in species occupancy or abundance. This is unfortunate, because they provide functional indicators of species-specific sensitivity to disturbance for conservation practitioners managing biodiversity in anthropogenic landscapes.

Here, we use intensive field surveys of bird communities across an agricultural land use gradient in the Peruvian Andes to identify functional response traits and changes to the ecological niche underlying community disassembly. Using speciesspecific abundances corrected for detectability as well as community-wide species lists generated from multiple standardized survey methodologies and field-collected morphological measurements, we link specific trait combinations with distinct biological processes to provide mechanistic insights into the drivers of community disassembly beyond emergent patterns of functional diversity. Specifically, we ask the following questions: (1) Do functional response traits reflecting morphology, foraging behavior, diet, and environmental niche breadth predict changes in abundance in countryside habitats compared to forest?, and (2) Does ecological niche space expand or contract differentially among functional trait groups for communities occupying countryside habitats?

Hypothesis 1. First, we hypothesized that specific combinations of functional response traits predict changes in species abundance between forest and different countryside habitats. Specifically, we predicted that traits associated with dense understory vegetation and edge habitat (e.g., short, rounded wings and small eyes), as well as frugivorous, nectivorous and granivorous diets predict increased abundances in early successional and mixed intensity agricultural habitats. Within fragments, we predicted that abundance changes would be best explained by traits related to area sensitivity and dispersal ability, specifically body mass, tarsus, and wing shape. Finally, we predicted that species with wider elevational range limits and greater habitat breadth (e.g., generalist species) would be less sensitive to agricultural disturbance due to having evolved across a broader range of floristics, vegetational structures, and microclimates.

Hypothesis 2. Second, we hypothesized that differential changes to ecological niche space following agricultural disturbance are driven by the expansion and contraction of distinct functional trait groups. Specifically, we predicted that the ecological niche space occupied by forest vs. countryside bird communities would expand and contract differentially among functional trait groups, with unique components of ecological niche space similarly expressed differentially in forest vs. countryside habitats depending on the group of traits. Furthermore, we expected that species with the most unique functional trait combinations would drive such changes,

with the prediction that species-specific functional originality would positively relate to niche expansion.

MATERIALS & METHODS

Study Design

We studied Andean cloud forest bird communities in northern Peru between 5-7°S and 77–79°W in the department of Amazonas, a region experiencing ongoing land use conversion due to increased road access. We used a block study design spanning an 1800–3100 m range of elevation sampled at approximately 200-m intervals (Figure S1). Cloud forests were characterized by a humid highland climate with mean annual temperatures of 10–17°C and mean annual rainfall 1000–1500 mm (Newell et al., 2022). We sampled seven landscapes at least 10 km apart across four watersheds spanning a 10,000 km² area. Within each landscape block (approximately 10-km²), we stratified sampling among four habitat types located within the same 300-m elevation band: contiguous mature forest connected to the Andean cordillera, isolated fragments of mature forest, regenerating early successional forest, and agricultural matrix ("silvopasture"). Given that Andean bird communities change rapidly with elevation, this type of "block impact-reference design" allowed us to compare changes in bird communities between forest and countryside habitats without the confounding influence of elevation (Morrison et al., 2008).

Fragments were generally small (median size: 4.35 ha; range: 0.8–219 ha), surrounded by a matrix of mixed-intensity agriculture, and located within 2 km of contiguous forest (mean distance: 972 m; range: 90–2500 m). Based on analysis of Landsat imagery and conversations with landholders, fragments had been isolated 15– 30+ years. Early successional forest sites were >30 ha tracts of regenerating pasture (15–30 years after abandonment) with dense stands of 2–3 m tall saplings and scattered residual trees. Silvopasture consisted of mixed intensity agricultural plots (mainly pasture, potatoes, and vegetables) interspersed with residual shrubby vegetation ("fencerows") and remnant mature "pasture trees" > 10cm DBH. To emphasize the effects of different types of relict woody vegetation on avian functional trait diversity, we noted each bird's location during surveys in silvopasture as either "fencerows", "pasture trees", or "pasture". In total we sampled 46 sites; we sampled contiguous forest and 2 - 6 forest fragments in all seven landscapes and early successional forest and silvopasture in five landscapes (Table S1).

Bird Survey Methods

We quantified the bird community using three survey techniques to reduce detection error related to species-specific behavior: point counts, flock surveys, and mist netting. Surveys were conducted from May–December 2016–2017 which largely coincided with the dry and transitional seasons and encompassed breeding activity for most species. See Appendix 2 for details.

In subsequent analyses we included detections for all species, except those for which our survey protocols were not designed, such as nocturnal species, raptors, and other wide-ranging species that regularly flew at high altitudes across entire landscapes containing multiple habitat types (i.e., swifts and parrots) (Gilroy et al., 2014). We included migratory species in our analysis because they were present in the study region for at least half of the sampling period. Unlike in the northern Andes, migratory species contributed a minor component of the bird community and were limited to three Nearctic migrants (*Catharus ustulatus, Setophaga canadensis, Setophaga fusca*), one austral/interandean migrant (*Turdus nigriceps*), and two frugivorous species with partial altitudinal migration (*Chloropipo unicolor, Mionectes striaticollis*).

We noted all detections during surveys in silvopasture as being in one of three habitat types: fencerows, pasture trees, and pasture. Our initial analyses indicated that functional traits aligned differently among the three habitats, with distinct adaptations to shrubby remnants ("fencerows") vs. relict trees ("trees") vs. open pasture ("pasture"). Hence, we present results for these three distinct habitats in addition to the full silvopasture bird community.

Functional Traits

We compiled a matrix of nine morphological and seven nonmorphological traits for all species encountered in our study system (Table 1). Morphological traits included documented ecomorphological relationships between form and function for foraging morphology (wing, tail, eye), dispersal morphology (tarsus, handwing index, body mass), and dietary morphology (bill length, width, and depth) (e.g., (Ausprey et al., 2021; Fitzpatrick, 1985; Forstmeier & Kessler, 2001; Landmann & Winding, 1993; Marchetti et al., 1995; Pigot et al., 2020; Sheard et al., 2020; Wheelwright, 1985). Morphological traits were sourced from field measurements at our study sites in northern Peru and supplemented by additional measurements from museum specimens. We used published databases for diet (three principal component axes from dietary percentiles in Elton Traits), foraging behavior (mean foraging stratum and number of strata), and elevation range breadth (Quintero & Jetz, 2018; Wilman et al., 2014). All traits were continuous quantitative metrics, which facilitated their use as predictive variables for species-specific abundance change among habitats. See Appendix 1 for details on trait compilation. Animals were handled in accordance with University of Florida Institutional Animal Care and Use Committee (IACUC) protocol #201508764. All fieldwork was conducted with permission from the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) in Peru (permit #221-2016-SERFOR-DGGSPFFS).

ANALYSIS

Hypothesis 1: Functional Predictors of Abundance Change

We quantified the degree to which functional traits predicted species-specific changes in abundance between forest and each countryside habitat using detailed abundance data from point count surveys. First, we used single-species hierarchical distance sampling models to estimate species-specific abundances while accounting for imperfect detection (Kèry and Royle 2015, Sollmann et al. 2016, Yamaura and Royle 2017). The model was looped across species (N = 194) to ensure that abundance estimates were independent among species (Appendix 4). As part of the model the abundance of species *i* at site *j* (λ_{ij}) was modeled as a log-linear function incorporating covariates for habitat (HAB), fragment size in log hectares (HA), and elevation (ELEV). PTS was an offset controlling for the number of points surveyed at each site. Forest was used as the baseline (intercept; $\beta_{0,i}$) against which to compare abundances of species for all other habitat levels ($\beta_{1,i}$):

$$\log(\lambda_j) = \beta_{0,i} + \beta_{1,i} HAB_j + \beta_{2,i} HA_j + \beta_{3,i} ELEV_j + \log(PTS_j)$$
(eqn 1)

The model was run twice for each species with detections in silvopasture either pooled as one habitat category or separated into three categories (fencerows, trees, and pasture) for a total of four and seven habitat levels, respectively, for each model run.

We used the species-specific habitat beta coefficients (derived from $\beta_{1,iin}$ Equation 1) to quantify the change in abundance between forest and each countryside habitat. We then tested whether each functional trait predicted abundance changes for each habitat type via a Bayesian meta-analysis (Kéry and Royle (2015)) (Appendix 4). Collectively, we tested whether each functional trait predicted abundance changes while both propagating uncertainty in the species-specific habitat beta estimates from the hierarchical community distance sampling model and incorporating phylogenetic structure to account for nonindependence in residual variation (Frishkoff et al., 2017). We repeated this process twice, including and excluding hummingbirds (family Trochilidae). We considered traits predictive of abundance changes if 90% of the posterior distribution for the regression slope of each trait and countryside habitat combination was less than or greater than zero.

Hypothesis 2: Ecological Niche Space & Community Overlap

Sample Coverage

For our analysis of ecological niche space occupied by each community, we extended our approach to include occurrences for species detected across all survey methods (N = 234 species). Because our intensive study design using multiple survey approaches was developed to overcome species detectability issues through depth of sampling effort, we were able to produce a near-complete inventory of the bird

community found at each habitat type within the specified elevation band. This was critical for including the full variation in functional trait diversity found within communities at each site, which would have been compromised if using small sampling plots that subset the full bird community. We assessed the effectiveness of our effort by calculating the sample coverage of each site, using each individual point visit, flock encounter, and net day as repeated sampling efforts (package 'iNEXT'; Chao & Jost, 2012). Sample coverage implicitly accounts for the fact that communities of different richness require different amounts of sampling effort to reach the asymptote of the species accumulation curve. This was important given that our sampling effort within fragments was necessarily smaller than in other habitats in order to maintain an equal amount of effort per unit area and time. Sample coverage was \geq 90% for all sites except six small fragments where it was > 75% (Figure S2).

Ecological Niche Space

We used species lists generated across the three survey methodologies to model the ecological niche space occupied by bird communities at each site for the six functional trait groups listed in Table 1. We used hypervolumes, because they provide an intuitive way of quantifying the range of traits exhibited by a given community and explicitly embrace Hutchinson's concept of *n*-dimensional ecological niche space (i.e., the "*n*-dimensional hypervolume") (Blonder et al., 2014; Hutchinson, 1957; Mammola & Cardoso, 2020). We calculated the volume of each hypervolume per functional trait group and site using the functions 'kernel.build' and 'kernel.alpha' in the package 'BAT' (method 'box', distance 'gower'; Cardoso et al., 2015). This calculation represents the total ecological niche space occupied by a community and is the same procedure for

quantifying functional diversity or functional trait volume using hypervolumes. We also calculated the standardized effect size (SES) of ecological niche space, which controls for species richness artifacts by comparing observed values against a null distribution of 100 randomly permuted communities (Appendix 3). We used presence-absence data because we were interested in documenting trait combinations on a species rather than individual level.

We ran additive linear models comparing the change in raw and SES ecological niche space between forest and each habitat while incorporating log fragment size as a covariate using a Bayesian MCMC sampling approach (function 'MCMCglmm' in package 'MCMCglmm') (Hadfield, 2010).

Community Overlap & Species Contributions

To quantify whether forest and countryside communities occupied unique areas of ecological niche space we joined hypervolumes between each pair of forest and countryside sites. We did so only within landscapes to ensure that differences in ecological niche space were not influenced by elevation. We then calculated the proportion of each joined hypervolume unique to forest and the proportion unique to the countryside habitat of interest (package 'hypervolume') (Blonder et al., 2014). Portions unique to forest and countryside habitats represented ecological niche space lost and gained, respectively, to agricultural land use conversion. We then plotted the sitespecific pairwise values of niche space unique to forests and countryside habitats, as well as their means and 95% confidence intervals.

We then evaluated the degree to which species-specific contributions to functional trait diversity explained ecological niche expansion and contraction of communities in forest v. countryside habitats. We first calculated the unique contributions each species made to the ecological niche space occupied by communities in forest, early successional vegetation, and silvopasture across the entire study region using the function *kernel.originality* in the package BAT (Cardoso et al., 2015). This function calculates the degree of species "uniqueness" or "originality" as the mean distance from the position of each species within a site-specific hypervolume to a sample of random points defining the hypervolume. Species with larger values contribute more to ecological niche space of the community occupying that site than those with smaller values. We then systematically removed a maximum of one species at a time from each forest site for foraging and dispersal morphological traits and from each early successional and silvopasture site for diet and dietary morphology and recalculated the amount of ecological niche space unique to each habitat. Finally, we regressed species originality values against the amount of ecological niche space gained when including each species using phylogenetic maximum likelihood regression (function *phylolm*; package 'phylolm') (Tung Ho & Ané, 2014). Through this procedure we explicitly examined how specific species contributed to niche expansion of foraging and dispersal traits in forests vs. countrysides and dietary traits in countrysides vs. forests.

Effects of Hummingbirds

Compared to all other species in our study region hummingbirds (family Trochilidae) possess strikingly unique morphological combinations, including the smallest tarsi and body masses, wings with the pointiest shape, and the longest culmen to body mass ratio of nearly all species (Figure S3). Given that they represent a Accepted Articl

sizeable component of the regional species pool (13%; 30/234 species), we were concerned that their unusual morphologies might obscure emergent properties for the remaining bird community. This is especially important for the set of dispersal traits, given that their body mass, tarsi, and wing shape likely relate more with extreme foraging adaptions (i.e., extended hovering and complex aerial maneuvers) than strict dispersal ability. For these reasons, we reported analyses that both include and exclude hummingbirds.

RESULTS

Hypothesis 1: Functional Predictors of Abundance Change

Our first hypothesis, that specific functional trait combinations differentially predict abundance changes between forest and countryside habitats, was largely supported (Figures 1 & 2). The relationship between abundance change and different functional trait groups exhibited low to moderate phylogenetic signal (Pagel's $\lambda = 0.12 - 0.69$), with signal tending to be lowest for fragments and highest for silvopastoral habitats (Table S4).

Foraging Morphology. Species that increased in abundance within fragments and the two shrubby understory habitats (early successional vegetation and fencerows) had short wings (Figures 1A & 1B). Large fragments hosted species with longer wings, which was mirrored by the results for the handwing index when excluding hummingbirds. Species in all countryside habitats had smaller eyes compared to those in forests. Accepted Articl

Dispersal Morphology. Species increasing in all countryside habitats except pasture had smaller body masses compared to forest, and body mass was positively related to fragment size (Figures 1A & 1B). Fragments, early successional vegetation, silvopasture, and fencerows housed communities with short and rounded wings, whereas species using trees in silvopasture had longer pointier wings. Likewise, species that increased in early successional vegetation and fencerows had longer tarsi compared to forests, whereas in silvopasture trees species had smaller tarsi. Including hummingbirds in the analysis tended to obscure the relationship between wing metrics and abundance in fragments and countryside habitats.

Dietary Morphology & Diet. Bill depth and width were the main indicator traits for morphology and were larger for species that increased in abundance in early successional vegetation and all silvopasture habitats (Figure 2). Results were similar for diet as insectivorous diets tended to decline across all habitats excepting fragments, while species possessing plant-based diets and specializing in nectivory or granivory increased. Frugivory did not change substantially for any habitat.

Foraging Behavior. Species in all agricultural habitats except pasture trees were composed of species that foraged at lower canopy strata (Figure 2). The number of strata used was not predictive except for pasture communities, which tended to house species with limited breadth of foraging strata.

Environmental Niche Breadth. Species that increased in all countryside habitats had wider elevational ranges and habitat breadth compared to forest species (Figure 2).

Hypothesis 2: Ecological Niche Space, Community Overlap, & Species Originality

Niche Space. Our second hypothesis, that differential expansions and contractions in ecological niche space occur in countryside habitats, was strongly supported. The niche space of foraging and dispersal morphology contracted in most countryside habitats, especially when controlling for species richness differences (Tables S5-S6; Figures 3 & 4). In particular, the SES of hypervolume size for dispersal traits in several fragment and silvopasture sites approached or exceeded the negative tails of the null community distributions, indicating extreme filtering of dispersal traits. Ecological niche space increased with fragment size for foraging ($\beta = 3.9$, P = 0.05) and dispersal morphology ($\beta = 9.3$, P = 0.002).

We observed the opposite pattern for dietary morphology and diet itself; the SES for ecological niche space significantly increased in most countryside habitats compared to forests (Figures 3 & 4). Communities in forests and fragments generally had extremely negative SES values, indicating strong filtering of traits related to diet and bill morphology. SES values were also more negative in larger fragments (β = -0.4, *P* < 0.001).

Likewise, niche space for foraging strata and environmental niche breadth increased in most countryside communities, with many sites in forests and fragments being highly filtered compared to the null expectation (Figure 4). Species occupying countryside habitats had significantly broader elevational range limits and habitat breadth compared to those within forests (Figures 5 & S7). For species in countryside habitats, mean elevational range limits were 20-60% wider than for forest species. Environmental breadth decreased in larger fragments ($\beta = 11.4$, P = 0.042).

Community Overlap. Communities in forest occupied large amounts of unique ecological niche space related to foraging and dispersal morphology compared to countryside habitats (Figure 6). The reverse was observed for dietary morphology and diet itself, for which communities in countryside habitats occupied unique components of niche space compared to forests. Interestingly, dietary overlap varied widely among fragments, reflecting a wide gradient of differentiation ranging from extreme loss to substantial gain in niche space. When considering environmental niche breadth, countryside habitats contained significantly larger amounts of unique ecological niche space compared to forest given that species in the agricultural matrix tended to have broader elevational ranges and use a larger diversity of habitat types.

Species Originality. Species originality strongly predicted the amount of unique ecological space found in forests across the study region for foraging and dispersal morphology and countryside habitats for dietary morphology and diet itself (Figure 7). After controlling for phylogeny there was a positive relationship between species originality and niche expansion of bird communities within forests vs. early successional (foraging: $\beta = 19.3$, P < 0.01, $\lambda = 0.72$; dispersal: $\beta = 38.1$, P < 0.001, $\lambda = 0.23$) and silvopastoral habitats (foraging: $\beta = 32.2$, P > 0.001, $\lambda = 0.45$; dispersal: $\beta = 38.5$, P < 0.001, $\lambda = 0.35$), meaning that species with the most functionally unique trait combinations contributed the most to unique components of ecological niche space found within forests. For dietary traits, species originality predicted ecological niche expansion in early successional (dietary morphology: $\beta = 52.5$, P < 0.001, $\lambda < 0.01$; diet: $\beta = 28.1$, P < 0.001, $\lambda = 0.26$) and silvopastural habitats (dietary morphology: $\beta = 24.6$,

P < 0.001, λ =0.96; diet: β = 31.7, *P* < 0.001, λ = 0.30). The patterns were similar when repeating the analysis separately for each landscape (Figure S8).

DISCUSSION

We detected substantial evidence for variation in the ecological niche space occupied by countryside bird communities. Functional predictors of abundance change varied distinctly among countryside habitats, with unique trait combinations emerging for specific remnant habitat structures. Early successional and silvopasture habitats displayed reduced amounts of ecological niche space for foraging and dispersal traits, with expansions for diet and environmental niche breadth. Species adapted to a wider range of habitat structures, floristics, and microclimates appeared less sensitive to disturbance.

Functional Response Traits: Fragments

Abundance within fragments was largely tied to dispersal traits, with fragments containing lower abundances of large-bodied species. This likely reflects wider home range requirements of larger species and mirrors global results showing their heightened sensitivity to fragmentation (Bregman et al., 2014; Brown & Sullivan, 2005; Kattan et al., 1994). Interestingly, the hypothesis that understory species with short rounded wings disappear from fragments due to dispersal limitation was rejected (Sekercioglu et al., 2002). The hand-wing index, a widely accepted morphological proxy for dispersal ability (Sheard et al., 2020), was negatively related to abundance changes in fragments, meaning that fragment isolation did not filter for species with

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morphological adaptations to extended flight. Instead, adaptive benefits associated with increased maneuverability in shrubby edge habitats as provided by short, rounded wings may have posed a stronger filter. Unlike fragments in other parts of the Andes that have been isolated for long periods of time (e.g., > 100 years) and lost species with poor dispersal ability (Gómez et al., 2021), fragments in our system were relatively young (< 30 years since isolation) and generally located within 1 km of large contiguous tracts of primary cloud forest. For these reasons they may still owe an extinction debt to be paid as time and continued deforestation interact to further isolate remnant bird communities (Halley et al., 2016).

Interestingly, we documented no associations between dietary traits and abundance changes in fragments. This runs counter to substantial literature emphasizing the loss of insectivores and large frugivores within fragments. (Kattan et al., 1994; Renjifo, 1999, Bregman et al., 2014). However, many reported declines of insectivores emanate from lowland rainforest sites where obligate flocking and ant swarms following present behavioral dependencies easily compromised by fragmentation (Mokross et al., 2013; Stouffer & Bierregaard, 1995). Montane bird communities may be more behaviorally resilient to disturbance given that the strength of multi-species flock networks degrades with increasing elevation even within relatively undisturbed forests (Jones & Robinson, 2021; Montaño-Centellas, 2020). Finally, species that increased in larger fragments tended to have narrower environmental niche breadth, suggesting that large forest patches harbor bird communities more similar to those in contiguous forests that include species specialized to specific food resources, floristics, and microclimatic regimes. Smaller fragments likely contained more generalist species found within the surrounding agricultural matrix.

Functional Response Traits: Agricultural Habitats

Species that increased in abundance in early successional vegetation, fencerows, and pasture tended to have short and rounded wings and longer tarsi. This was predicted by research demonstrating the value of rounded wings to foraging maneuverability in structurally dense understories and long legs for terrestrial movement (Forstmeier & Kessler, 2001; Landmann & Winding, 1993). Likewise, these habitats harbored species with smaller eyes, which has been previously linked to habitat brightness (Ausprey et al., 2021; Martinez-Ortega et al., 2014). Species increasing in abundance also had thicker bills, understory foraging behaviors, and plant-based diets based on nectar and seeds. This is consistent with edge habitats harboring early successional microhabitats producing abundant flowers, fruits, and seeds and avian species morphologically adapted for plant-based diets (Diaz, 1990; Restrepo et al., 1999; Wheelwright, 1985). Finally, species were strongly filtered based on their foraging height, with canopy species disappearing in shrubby understory habitats lacking an overstory.

Our decision to repeat the analysis when excluding hummingbirds and dividing silvopastoral observations into specific habitat elements yielded unique results. First, removing hummingbirds exposed the relationship between wing length and shape for fragments and silvopasture habitats, as well as emphasizing clear losses in dispersal morphology outside of forests. Hummingbird species have completely different dispersal traits compared to other species increasing in shrubby habitats (long, narrow wings and short tarsi) due to their unique ability to hover while taking nectar (Dakin et al., 2018). Given that many hummingbirds extensively use edge habitats (Feinsinger, 1978), their unique morphologies masked the fact that most other species were adapted to have short, rounded wings and long tarsi for maneuverability in dense shrubs and terrestrial movement. Second, subdividing the bird community within the agricultural matrix (silvopasture) unveiled several detailed patterns supporting hypotheses related to ecological adaptations, specifically traits related to wing shape and tarsus length. In both cases pooling all detections into one silvopasture category obscured the fact that species using fencerows tend to have morphological adaptations in line with shrubby habitats and terrestrial movement (short rounded wings and long tarsi) while those in pasture trees have long pointy wings and short tarsi more effective for aerial foraging.

Ecological Niche Space & Community Overlap

Extensive research in agricultural landscapes across the world has demonstrated a widespread loss of avian functional richness, with limited indications of moderate niche expansion in some disturbed landscapes (Etard et al., 2022; Flynn et al., 2009; Matuoka et al., 2020). Our results, however, emphasize the importance of identifying distinct trait combinations of biological relevance that respond differently to disturbance. Specifically, we revealed a striking difference in functional diversity related to foraging and dispersal traits vs. traits related to diet and environmental breadth, with the former contracting and the latter expanding in disturbed habitats. Indeed, several forest and agricultural sites had extremely small and large standardized effect sizes, respectively, for ecological niche space related to diet, emphasizing a strong environmental filtering effect. This pattern was also seen in the results for community overlap, which showed expansions of unique niche space in agricultural habitats related to diet and environmental niche breadth, and losses related to foraging and dispersal. Hence, agricultural disturbance imposed environmental conditions that filtered species with maladaptive foraging and dispersal traits, while simultaneously providing expanded niche opportunities for species with diets dependent on edge-associated plant resources, such as nectar, fruit, and seeds. Such patterns were driven by speciesspecific contributions to functional diversity, with the most functionally unique species driving shifts in ecological niche space. Our results build upon a recent global analysis of vertebrate functional diversity that described both contraction and expansion of trait space in disturbed landscapes (Etard et al., 2022) by painting a more nuanced explanation of the exact biological drivers underlying such differential changes to the ecological niche.

Environmental Niche Breadth

Species with wide elevation range limits and broad habitat breadth increased in abundance in all countryside habitats, producing communities that occupied unique components of ecological niche space. Because ranges of Neotropical montane birds generally occupy distinct elevational bands (Pigot et al., 2016), species with wider elevational range limits presumably encounter a larger diversity of plant species, food resources, and climatic regimes. This likely makes such species more resilient when confronting novel environments, and upslope range shifts associated with climate warming are strongly associated with broad elevation ranges (Neate-Clegg et al., 2021). Collectively, our results support the idea that resource generalists adapted to diverse habitat structures, floristics, and microclimates are less sensitive to disturbance and are more resilient to abrupt changes in resources found within agricultural landscapes (Clavel et al., 2011; Julliard et al., 2004).

Conservation Implications

Tropical countrysides often contain altered floristics and habitat structures (Mayfield & Daily, 2005), and in our system agricultural disturbance both expanded and contracted ecological niche space available to biological communities. Conservation practitioners can enhance functional diversity in agricultural landscapes by maintaining a variety of native floristics and habitat structures that maximize ecological niche space via substrates for invertebrates and plant-based food resources such as flowers, fruit, and seeds. We particularly emphasize the importance of forest fragments and large tracts of early successional vegetation which maintained high levels of functional diversity in our system. We caution, however, that substantial amounts of functional diversity related to foraging and dispersal traits found within our contiguous forest sites were lost in agricultural habitats and that forests may enhance functional diversity within agricultural landscapes through their proximity. For example, past studies in the Andes have shown agricultural bird communities to contain more taxonomic and functional richness when closer to large tracts of contiguous forest (Cannon et al., 2019; Gilroy et al., 2014). Likewise, conceptual approaches that couple intact forest sites with high intensity agricultural plots (i.e., "spared landscapes") contain higher taxonomic and functional richness as well as larger number of species of conservation concern compared to mixed intensity agricultural (i.e., "shared landscapes") (Edwards et al., 2021). Hence, managing for biodiversity in agricultural landscapes is dependent upon both the scale of desired outcomes and the socio-economic and political realities of

developing consensus for habitat management among local landholders (Pagdee et al., 2006). While our results provide guidance for enhancing ecological niche space and associated functional diversity within mixed intensity agricultural landscapes, we emphasize the central role that intact forests play in maintaining unique elements of ecological function.

lan J. Ausprey and Felicity L. Newell conceived the ideas, designed the methodology, and collected the data; lan J. Ausprey analyzed the data and led the writing of the manuscript. Ian J. Ausprey, Felicity L. Newell, and Scott K. Robinson contributed critically to the drafts, provided funding, and gave final approval for publication. The data were collected in collaboration with student field assistants from Peru, Colombia, Bolivia, and Argentina, as well as local communities that provided logistical assistance. These individuals are listed in the Acknowledgments and Supplemental material.

AUTHOR CONFLICTS OF INTEREST

All authors declare no conflicts of interest.

DATA AVAILABILITY

All scripts and datasets are published at FigShare:10.6084/m9.figshare.19249235 (Ausprey et al. 2022).

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Tables & Figures

			Fragment	Early		Silvopasture	
Functional Group	Trait	Fragments	Size	Successional	Fencerows	Trees	Pasture
Foraging	Wing Chord			-	-		-
Morphology ¹	Tail Length			+	+		
	Lateral Eye Width			-	-	-	-
Dispersal	Tarsus Length			-	-	-	-
Morphology ¹	Handwing Index	+	-	-	-	+	-
	Mass	-	+				
Dietary	Exposed Culmen			-	-		-
Morphology ¹	Bill Width & Depth			+	+		+
	Bill Depth/Width			+	+		+
Diet (PC axes) ²	Invert vs. Fruit	-	+	-	-	-	-
	Seeds vs. Fruit			+	+		+
	Nectarvs. Other			+	+	+	-
Foraging	Mean Relative Height			-	-	+	-
Behavior ²	# Canopy Strata			-	-	-	-
Environmental	Habitat Breadth			+	+	+	+
	(# habitats across range)						
Niche Breadth ³	Elevational Range			+	+	+	+

Table 1. Six groups of functional response traits used in all analyses and predicted relationship with abundance changes between forest and countryside habitats based on published ecomorphological relationships (Fitzpatrick, 1985; Forstmeier & Kessler, 2001; Landmann & Winding, 1993; Marchetti et al., 1995). Data sources: ¹Field and museum measurements by the authors, ²Elton Traits database (Wilman et al., 2014), ³Bird Life International (habitat breadth) & Quintero and Jetz (2018) (elevational range). Traits were complete for all species.



Figure 1. Functional predictors of abundance change between forests and countryside habitats for morphological traits of species with detailed abundance estimates from point count surveys for (A) the full bird community (N = 194 species) and (B) excluding hummingbirds (N = 175 species). Traits relate to (a) foraging behavior, (b) dispersal ability, and (c) diet, Amazonas, Peru, 2016–2017. Violin plots represent the posterior distributions for the regression of each trait on mean abundance change. Orange indicates significantly negative relationship with abundance compared to forest, and green indicates significantly positive relationship (90% of posterior distribution to right or left of zero).





Figure 2. Functional predictors of abundance change between forests and countryside habitats for nonmorphological traits of N = 194 species with detailed abundance estimates from point count surveys. Traits reflect (a) diet, (b) foraging behavior, and (c) environmental niche breadth, Amazonas, Peru, 2016–2017. Orange indicates significantly negative relationship with abundance compared to forest, and green indicates significantly positive relationship (90% of posterior distribution to right or left of zero). Results when excluding hummingbirds were similar (Figure S4).



Figure 3. Ecological niche space of avian communities in tropical montane forest and countryside habitats for morphological functional trait groups outlined in Table 1: (A) all species (N = 234), (B) excluding hummingbirds (N= 204). Percent change in ecological niche space compared to forest and the standardized effect size (SES) compared to forest are significant where **P \leq 0.05, *P \leq 0.1. Dashed lines indicate tails of the null community distribution (0.025 – 0.975), Amazonas, Peru, 2016 – 2017.





Figure 4. Ecological niche space of avian communities in tropical montane forest and countryside habitats for nonmorphological functional trait groups outlined in Table 1 (N = 234 species). Percent change in ecological niche space compared to forest and the standardized effect size (SES) compared to forest are significant where **P \leq 0.05, *P \leq 0.1. Dashed lines indicate tails of the null community distribution (0.025 – 0.975), Amazonas, Peru, 2016 – 2017. Results when excluding hummingbirds were similar (Figure S5).



Figure 5. Mean (+/- 95% CI) elevational range breadth for N = 234 species occupying forest and countryside habitats, Amazonas, Peru, 2016–2017. Three forest endemics (*Scytalopus femoralis, Grallaria przewalskii, Piprela pulchra*) and three open-country species (*Zonotrichia capensis, Turdus capensis, Pheucticus chrysogaster*) illustrate examples of species with narrow and wide elevational range limits. Results for fencerows and pasture trees were similar to silvopasture and are omitted for simplicity. Photos are reproduced under Creative Commons licenses or provided with permission by the photographer: Ian Ausprey, Jon Irvine, Jorge Montejo, Tom Murray, Brian Ralphs.



e Figure 6. Ecological niche space unique to bird communities occupying forests or countrysides habitats for functional trait groups outlined in Table 1, Amazonas, Peru, 2016 – 2017 (N = 234 species). Each dot represents a single pair of overlapping hypervolumes for communities in forest vs. the specific countryside habitat, with units being the proportion of hypervolumes unique to each habitat. Fragment points are scaled to patch size. Large dots are means +/- 95% CI across sites. Data for fencerows and pasture trees were similar to silvopasture and were omitted for simplicity. Results when excluding hummingbirds were similar (Figure S6).



Figure 7. Species with unique functional trait combinations increased the amount of unique ecological niche space occupied by communities in forests and countryside habitats in Amazonas, Peru, 2016 – 2017. Examples are shown for foraging (*Grallaria squamigera, Nothocercus nigrocapillus, Odontophorus speciosus*), dispersal (*Aburria aburria, Pharomachrus auriceps, Ocreatus underwoodi*), and dietary morphology (*Ensifera ensifera, Pheucticus chrysogaster, Diglossa mystacalus*), as well as diet (*Catamenia analis, Spinus magellanicus, Amazilia chionogaster*). All regressions are significant (P < 0.05) while controlling for phylogeny. Photos are reproduced under Creative Commons licenses or provided with permission by the photographer: Thibaud Aronson, Ian Ausprey, Tom Cantwell, David Cook, Carlos Enrique, Ron Knight, Patty McGann, Andy Morffew, Brian Ralphs, Joseph Smit, Felix Uribe, Arley Vargas.