

Dispersal limitation predicts the spatial and temporal filtering of tropical bird communities in isolated forest fragments

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Abstract

1. The link between dispersal traits and patterns of community assembly remains a frontier in understanding how vertebrate communities persist in fragmented landscapes. Using experimental release trials and intensive field surveys of bird communities in fragmented forests of the Peruvian and Colombian Andes, we demonstrate that morphological traits related to movement (1) predict experimental flight performance and (2) exhibit dispersal-mediated environmental filtering at the community scale.
2. After correcting for body size, four traits hypothesised to influence flight ability (wing length, wing pointedness, wing loading, and eye size) predicted distance flown across a hostile experimental landscape, with successful species having significantly longer pointed wings, carrying less mass per unit wing area (i.e. lower wing loading), and having smaller eyes. Species with larger eyes also displayed increased flight latency, potentially due to disability glare.
3. At the community scale, we detected a gradient of dispersal-mediated environmental filtering in fragments compared to reference forest within the same landscape, with relative differences in trait values explained by the temporal and spatial extent of patch isolation. In the Colombian landscape where fragments had been isolated for >60 years, communities were filtered for species with long and narrow wings and small eyes, especially within the most spatially isolated fragments. We observed the opposite pattern in the more recently fragmented Peruvian landscape (15–30 years): communities within fragments tended to have shorter and more rounded wings compared to those in nearby contiguous forests, suggesting that dispersal-limited species accumulate in the initial years following patch isolation due to “restricted dispersal” and represent an extinction debt yet to be paid.
4. Our results (1) experimentally validate the use of morphological traits as proxies for movement ability in fragmented landscapes, (2) demonstrate that visual acuity functions as a novel dimension of dispersal limitation and (3) quantify how the spatial and temporal components of patch isolation produce a gradient in dispersal-mediated environmental filtering and extinction debt for communities inhabiting fragments.

KEYWORDS

bird, dispersal, extinction debt, eye, fragment, handwing, isolation, tropical

1 | INTRODUCTION

The ability of organisms to move or disperse among habitat patches is critical to the functioning of metapopulations within anthropogenic landscapes (Hanski & Ovaskainen, 2000). Fragmentation, in particular, poses novel spatial constraints that are thought to filter for functional traits related to an organism's ability to move and navigate among habitat patches (Gómez et al., 2021; Weeks et al., 2023). Understanding how dispersal-mediated environmental filtering contributes to community disassembly in disturbed landscapes requires understanding how functional traits related to movement vary across fragments of different spatial and temporal isolation.

Birds are largely aerial organisms, and most species prospect for suitable habitat from the air (e.g. Cooper & Marra, 2020; Cox & Kesler, 2012). Flight efficiency can be defined by the lift to drag ratio, which quantifies the amount of aerodynamic power being produced in relation to the sum of induced drag generated by lift, profile drag arising from the wings and parasite drag caused by the body (Norberg, 1990; Rayner, 1979a). Induced and profile power are particularly important for birds navigating among habitat patches in fragmented landscapes (Norberg, 1990) as they collectively describe the work required to generate lift and weight support for thrust required during take-off and slow, forward flight.

Central to calculating these metrics are measurements that quantify wing size and shape and efficiency of mass transport, including aspect ratio and wing loading, respectively (Norberg, 1990, 2002). Wings of high aspect ratio are longer and pointier and improve flight efficiency by increasing the lift to drag ratio and reducing energy expenditure, especially at slow speeds (Norberg, 1990; Rayner, 1988). Short and rounded wings of low aspect ratio sacrifice flight efficiency for improved manoeuvrability in closed or cluttered environments (Norberg, 2002). Wing loading quantifies the amount of mass carried per unit area of the wing and is similar to disc loading, which measures the pressure force exerted over the wing (Norberg, 2002; Rayner, 1979b). Species with low wing loading minimise the induced power required to take-off and fly over long distances, whereas species with high wing loading compensate either with high aspect ratio wings that achieve faster flight speeds (e.g. ducks) or large muscle mass that powers increased acceleration during take-off (e.g. grouse; Norberg, 1990). In sum, flight efficiency is maximised by low wing loading and high aspect ratio wings that cumulatively reduce disk loading and aerodynamic power requirements during take-off and while maintaining flight (Rayner, 1979a). For this reason species specialising in long-distance migratory and dispersal movements and using aerial foraging manoeuvres (e.g. sallying and hovering) have high aspect ratio wings (Baldwin et al., 2010; Claramunt, 2021; Dawideit et al., 2009; Fitzpatrick, 1985; Forstmeier & Kessler, 2001; Kaboli et al., 2007; Landmann & Winding, 1993; Lockwood

et al., 1998; Marchetti et al., 1995; Saino et al., 2010), demonstrating the pervasive influence of wing morphology in driving flight performance from small-scale foraging behaviours to large-scale dispersal movements (Weeks et al., 2022).

The ability of an organism to navigate through complex landscapes is further affected by functional traits that regulate its perceptual range (Lima & Zollner, 1996). Birds are highly visual organisms, and the eye is presumably the primary anatomical structure that birds use to navigate among habitat patches. Larger eyes improve visual resolution and sensitivity by increasing both the focal length and pupil aperture such that species adapted to dark environments, aerial foraging manoeuvres, and diets requiring prey recognition at long-distance have larger eyes after correcting for body mass allometry (Ausprey, 2021; Garamszegi et al., 2002; Martin, 1999; Thomas et al., 2002). While larger eyes might be assumed to improve the perceptual range via enhanced recognition of distant habitat patches, they may also prove maladaptive if confronted with abrupt transitions in brightness associated with highly fragmented landscapes (Stratford & Robinson, 2005). Birds are susceptible to glare (Fernandez-Juricic et al., 2012), and species with relatively larger eyes adapted to the dark forest interior are sensitive to brightly lit anthropogenic landscapes (Ausprey et al., 2021; Martínez-Ortega et al., 2014).

While experimental translocations in fragmented landscapes demonstrate that the connectedness and amount of remnant habitat patches influences individual movement trajectories (Belisle et al., 2001; Castellón & Sieving, 2006; Hadley & Betts, 2009), the subsequent dispersion of functional traits related to locomotion for communities persisting in isolated fragments remains less clear. In contrast to bats, in which species with higher aspect ratio and lower wing loading are more likely to forage in anthropogenically disturbed habitats with reduced clutter (Frank et al., 2017; Núñez et al., 2019), studies of birds in isolated forest fragments at local scales have shown no or weak signals of dispersal-mediated environmental filtering based on trait distributions (Bovo et al., 2018; Bregman et al., 2015). This contrasts with a recent global analysis that links dispersal limitation based on wing shape to increased edge sensitivity (Weeks et al., 2023). One possible reason for the lack of clear patterns is that fragmentation studies often fail to account for the temporal dimension of patch isolation. For example, one study of a single fragment in the Colombian Andes showed the temporal trajectory of dispersal traits over 100 years of isolation. Extinctions of species with limited mobility (short-rounded wings) were offset by the colonization of highly mobile species (long-pointed wings), producing significant changes in the dispersion of dispersal traits over time (Gómez et al., 2021).

Given the extreme logistical limitations of studying dispersal over multiple species of small songbirds at large spatial scales, dispersal challenge experiments have been used as an experimental proxy to identify morphological traits associated with species-specific

extinctions, distributional range boundaries, population connectivity and genetic structure linked to natural barriers to movement among populations, such as islands and rivers (Claramunt et al., 2012; Hartfelder et al., 2020; Moore et al., 2008; Naka et al., 2022). However, no study has explicitly linked experimental evidence for flight performance to the dispersion of functional traits related to movement among isolated forest fragments. Here, we use experimental release trials coupled with intensive community surveys in two Andean landscapes with contrasting fragmentation histories (recent vs. long-term patch isolation) to explicitly test the hypothesis that dispersal traits predict flight performance and sensitivity to patch isolation for tropical montane forest bird communities in fragmented landscapes.

First, we hypothesised that morphological traits related to movement predict experimental flight performance. Specifically, we predicted that species with smaller eyes and longer, more pointed wings that carry less mass per unit wing area (low wing loading) would fly farther and be more likely to successfully cross an open landscape. Furthermore, we predicted that species with larger eyes would experience increased flight latency upon release due to glare associated with extreme brightness in agricultural landscapes. Second, we hypothesised that communities inhabiting isolated forest fragments would exhibit dispersal-mediated environmental filtering, with the prediction that fragments compared to nearby contiguous forests support communities having longer and more pointed wings and smaller eyes that facilitate movement across patchy, brightly lit vegetation within the surrounding landscape matrix. Furthermore, we predicted that communities within the most temporally and spatially isolated patches would exhibit the strongest signals of dispersal-mediated environmental filtering.

2 | METHODS

2.1 | Study systems and bird surveys

We used species occurrence data from two studies in the Peruvian and Colombian Andes that surveyed montane bird communities in countryside using similar designs and field approaches (Ausprey et al., 2022; Renjifo, 2001). Both used point count and flock surveys to quantify the full bird community occupying (1) small forest fragments (<30 ha) that had been largely undisturbed by humans and/or livestock and (2) nearby (<10 km) tracts of contiguous mature forest. Fragments were surrounded by a heterogeneous agricultural matrix containing pasture and crop fields, silvopasture and isolated shrubby elements (e.g. fencerows). In Colombia, half of the fragments were surrounded partially by exotic-tree plantations (cypress, pine and eucalyptus) that had been planted in pasture 15–30 years prior to surveys. The Peru sites were located in the Department of Amazonas, and the Colombia sites were located in the Departments of Quindío and Risaralda.

We selected these two study systems because they differed in the temporal isolation of fragments. The Peru fragments had been isolated 15–30 years prior to surveys, whereas fragments in Colombia

had been isolated >60 years. Critically, both studies were careful to control for other factors beyond patch isolation that might influence relative changes in species composition and dispersal trait distributions between fragments and nearby reference contiguous forests. First, they selected sites within the same landscape and elevational band, which isolated changes in community composition associated with fragmentation from those associated with elevational or regional species turnover. Second, both were careful to select fragments with minimal internal disturbance from humans and cows and contained habitat structures that did not differ significantly from nearby contiguous forests (Appendix 2; Table S2.1). Third, although exact species identities varied between the two regions (as we would expect given high rates of spatial turnover in the Andes), phylogenetic clades and associated trait distributions were similarly represented, ranging from dispersal limited clades such as tapaculos, antbirds and guans, to highly mobile groups, such as tanagers and hummingbirds (Figure 1). This meant that there were no systematic differences in trait distributions that might bias the detection of dispersal-mediated environmental filtering. Because low-latitude bird communities are typically dispersal-limited (Weeks et al., 2023), even with different regional species pools we would expect similar directional shifts in trait distributions within fragmented communities compared to forest.

Both studies had sufficient sample coverage to detect all species inhabiting all sites (Chao & Jost, 2012; Hsieh et al., 2022; Figure S1.1). A total of $N=192$ species were detected at montane sites in Amazonas, Peru and $N=165$ species in Quindío/ Risaralda, Colombia. In total, we included data for seven forest sites and 27 fragments in Peru and six forest sites and 16 fragments in Colombia. Details regarding survey methodology are in the works of Ausprey et al. (2022) and Renjifo (2001).

2.2 | Experimental release trials

We performed experimental release trials (e.g. Moore et al., 2008) at the forest margins of three agricultural landscapes in the same Peruvian study system. Trials occurred between 07:00–13:00 for eight days total across the years 2015–2017. Each site consisted of a cloud forest tract and pasture with no residual trees or shrubs. Within each pasture we placed a release station 100 m perpendicular from the forest edge. Each station consisted of the same release box mounted on a 1.5 m tripod, with the opening oriented directly toward the forest. We considered the area of pasture between the release box and forest edge to be a hostile “gap” simulating environmental conditions forest species in agricultural systems face when moving among isolated forest patches.

We captured birds using passive mist netting procedures within forest tracts adjacent to the release stations. We then banded individuals and rapidly recorded their age and morphology before moving them to the release box within 30 min of capture. We placed each bird in the release box, closed the door and waited a 2-minute “calming” period, noting percent cloud cover, wind speed (Beaufort Scale), and light intensity using a light meter. We opened the door

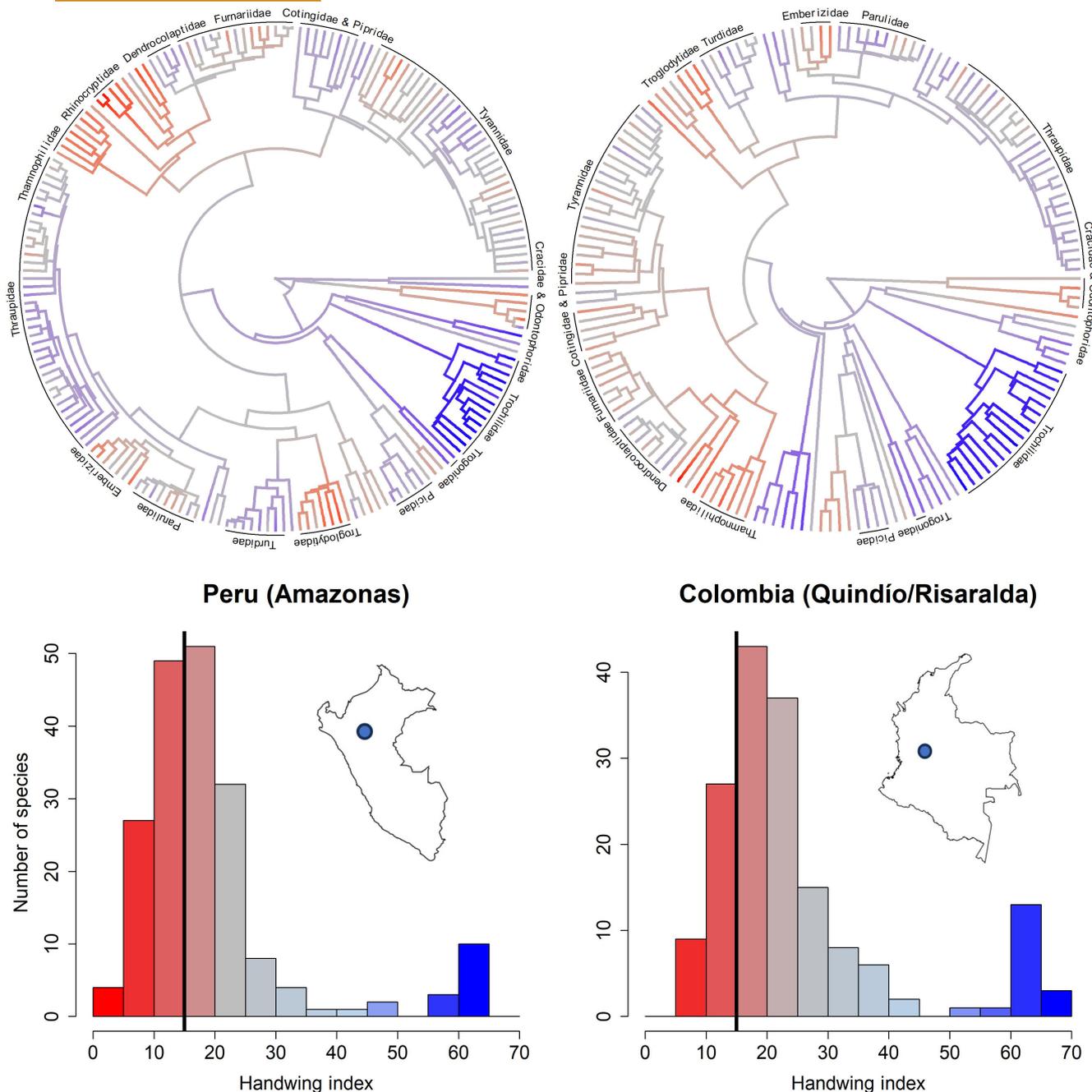


FIGURE 1 Phylogenies and distributions of the handwing index for regional species pools studied in Amazonas, Peru ($N=192$) and Quindío/Risaralda, Colombia ($N=165$). The vertical lines represent potential aerodynamic thresholds in flight capacity based on release experiments.

from behind and timed how long the bird took to leave the box in seconds ("flight latency"). If a bird delayed >120 s we gently tapped the box from behind for 10s until the bird flew.

Upon flight from the box we watched each bird with binoculars until it either reached the forest ("succeed") or flew to the ground ("fail"). Because we were only testing forest species, we were not expecting individuals to interact with pasture unless they were unable to complete the test flight. We recaptured all "failures", quickly measured distances to the release box with range finding binoculars, and then returned all individuals to the

forest area where they were captured. We only performed trials during mornings with no rain and little to no wind (Beaufort Scale ≤ 2). In total we released $N=77$ individuals of $N=36$ species (Table 1). Eleven birds (14%) were subsequently captured after experiments (including six in subsequent years), suggesting little impact of the experiment on their survival. Mist-netting and experiments were conducted according to IACUC protocol #201508764 at the University of Florida and permitted by the Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) in Peru (# 221-2016-SERFOR/DGGSPFFS).

TABLE 1 Results from experimental release trials for $N = 37$ species of tropical montane birds, Amazonas, Peru, 2015–2017. Table includes number of successful trials in which an individual reached the forest, mean \pm SE distance flown (m), mean \pm SE delay/latency to leave the release box (sec) and five morphological traits associated with aerial movement (means, $N > 10$). Species which reached the forest on $>80\%$ of trials were considered successful in the analyses.

Family	Species	Success/individuals	Distance (m)	Delay (sec)	Residual wing length	Hand-wing index	Wing loading	Residual eye size	Mass (g)
Picidae	<i>Colaptes rivolii</i>	1/1	100	1	0.09	26.4	46.8	-0.04	85.1
Ramphastidae	<i>Aulacorhynchus prasinus</i>	1/1	100	1	-0.16	10.6	75.4	0.04	166.4
Trogonidae	<i>Trogon personatus</i>	1/1	100	61	0.17	38.2	44.6	0.08	55.7
Trochilidae	<i>Adelomyia melanogenys</i>	3/3	100 \pm 0	1 \pm 0	0.00	58.7	43.2	0.16	3.9
	<i>Coelligena torquata</i>	1/1	100	1	0.27	60.6	40.6	0.17	7.8
	<i>Boissonneaua matthewsii</i>	3/3	100 \pm 0	5 \pm 3	0.25	62.8	36.7	0.10	7.4
	<i>Helianthus viola</i>	1/1	100	1	0.13	61.8	38.5	0.13	5.6
	<i>Eriocnemis alina</i>	4/4	100 \pm 0	29 \pm 13	0.02	61.4	36.4	0.20	4.1
Tyrannidae	<i>Mionectes striaticollis</i>	1/1	100	3	0.00	14.3	25.3	0.02	13.8
	<i>Pseudotriccus ruficeps</i>	0/1	29	6	-0.12	10.1	26.0	0.16	11.9
	<i>Zimmerius viridiflavus</i>	1/1	100	1	-0.10	12.8	23.3	0.03	10.4
	<i>Elaenia pallatangae</i>	1/1	100	1	0.07	18.9	24.2	0.06	15.9
	<i>Myiophobus flavicans</i>	0/2	40 \pm 10	5 \pm 2	-0.01	15.5	29.3	0.18	13.5
	<i>Ochthoeca pulchella</i>	0/3	36 \pm 2	26 \pm 18	-0.02	12.3	28.8	0.12	11.5
Cotingidae	<i>Pipreola riefferii</i>	0/2	62 \pm 11	4 \pm 2	-0.09	15.7	48.8	0.02	44.1
Thamnophilidae	<i>Drymophila striaticeps</i>	0/3	4 \pm 1	91 \pm 17	-0.22	6.50	42.8	0.05	12.6
Furnariidae	<i>Premnornis guttifer</i>	0/3	33 \pm 9	63 \pm 34	-0.03	12.9	27.9	0.05	15.2
	<i>Premnoplex brunescens</i>	0/1	7	91	-0.13	11.2	37.3	0.10	16.3
	<i>Margarornis squamiger</i>	1/1	100	3	0.08	19.1	27.9	-0.08	17.8
	<i>Syndactyla rufosuperciliata</i>	0/2	51 \pm 10	1 \pm 0	-0.03	13.0	36.1	-0.04	27.9
	<i>Xiphorhynchus triangularis</i>	1/1	100	3	0.19	21.9	27.0	-0.03	45.7
	<i>Lepidocolaptes lacrymiger</i>	1/1	100	1	0.23	22.0	30.4	-0.10	31.3
Rhinocryptidae	<i>Scytalopus femoralis</i>	0/2	2 \pm 1	19 \pm 3	-0.24	3.90	63.6	0.05	24.7
Corvidae	<i>Cyanolyca viridicyanus</i>	1/1	100	7	0.11	13.0	36.7	0.21	96.7
Turdidae	<i>Catharus fuscater</i>	0/3	68 \pm 8	8 \pm 4	-0.01	14.3	40.6	0.12	31.7
Troglodytidae	<i>Troglodytes aedon</i>	0/1	14	1	-0.23	9.40	37.9	-0.04	12.6
	<i>Troglodytes solstitialis</i>	0/2	21 \pm 7	3 \pm 1	-0.27	8.60	42.3	0.03	12.2
Parulidae	<i>Myioborus melanocephalus</i>	5/5	100 \pm 0	1 \pm 0	0.04	14.5	24.0	0.04	11.7
	<i>Myiothlypis nigrocristata</i>	1/1	100	61	-0.07	10.1	24.2	-0.02	12.9
	<i>Myiothlypis coronata</i>	9/11	85 \pm 8	8 \pm 7	-0.02	12.7	30.7	0.09	16.5

(Continues)

TABLE 1 (Continued)

Family	Species	Success/individuals	Distance (m)	Delay (sec)	Residual wing length	Hand-wing index	Wing loading	Residual eye size	Mass (g)
Thraupidae	<i>Hemispingus frontalis</i>	0/1	40	3	-0.02	13.0	35.6	-0.03	18.3
	<i>Thlypopsis ornata</i>	2/2	100±0	1±0	-0.02	15.4	25.5	-0.21	12.2
	<i>Thraupis cyanocephala</i>	1/1	100	3	-0.01	16.2	37.8	-0.08	31.4
	<i>Tangara vassorii</i>	1/1	100	2	0.03	22.8	31.1	-0.14	18.0
	<i>Diglossa albilatera</i>	2/2	100±0	2±0	-0.05	12.8	25.6	-0.09	11.1
Icteridae	<i>Cacicus chrysonotus</i>	1/1	100	3	0.18	16.6	31.3	-0.16	69.5
Emberizidae	<i>Atlapetes latinuchus</i>	2/5	66±16	13±8	-0.11	11.2	43.4	0.02	27.4

2.3 | Morphological traits

We selected five morphological traits that we hypothesised would predict experimental flight performance and/or dispersal-mediated environmental filtering for communities inhabiting isolated forest fragments: handwing index, residual wing length, wing loading, residual eye size and body mass. Measurements were sourced from the field, museum specimens, or published datasets (Ausprey, 2021; Tobias et al., 2022; Appendix 3).

3 | ANALYSIS

3.1 | Experimental release trials

We used phylogenetic linear regression to test the hypothesis that the five dispersal traits predicted the mean distance flown by each species (function 'phylolm' in package 'phylolm', Tung Ho & Ané, 2014). We assumed a model of evolution incorporating Pagel's lambda (λ_p) and using a consensus tree based on 100 hypothesised trees from a published avian phylogeny (Jetz et al., 2012) (function 'consensus.edge' in the package 'phytools', Revell, 2012). We controlled for variability in environmental conditions by including covariates for cloud cover, light intensity, and wind speed. We repeated the same procedure for a binary metric of whether the species was successful or not at reaching the forest using phylogenetic logistic regression models (function 'phyloglm' in package 'phylolm'), which include the phylogenetic correlation parameter α_p . Exploratory analyses suggested the existence of thresholds in the relationship between morphology and flight distance, and we statistically tested for this using segmented linear regression (function 'segmented' in package 'segmented', Muggeo, 2003, 2008).

3.2 | Dispersion of community dispersal traits

To quantify the degree and directionality of dispersal trait filtering, we compared trait dispersions between fragments and nearby reference forests within each of the two regions. This unique "paired" comparison allowed us to examine relative changes in community trait distributions between forests and fragments within each region while controlling for differences in species composition between the two regional species pools. Specifically, we first calculated the median values of the hand-wing index, residual wing length and eye size for the communities occupying each forest and fragment site and then compared median community trait values between forests and fragments within each region system using *t*-tests. We also used least-squares regression to test how patch isolation based on distance from forest and the extent of matrix habitat surrounding each fragment predicted variation in community dispersal traits among fragments while controlling for patch size and elevation. For the fragments in Peru, we quantified variation in matrix composition surrounding each fragment as the proportion of shrub and forest habitat found within a 1-km buffer. This

was calculated via a supervised image classification analysis in ArcMap based on Sentinel-2 imagery from 2017 and informed by the authors' extensive experience with land use practices in the same landscapes. We were unable to replicate this analysis for the Colombia dataset, because we did not have access to satellite imagery from the time when the surveys were completed. Instead, we included a binary variable indicating whether each fragment was surrounded entirely by pasture or by a mixture of pasture and exotic tree plantations. To control for potential biases associated with differences in species richness among study sites within each of the two regions, we ranked observed median values against distributions for 100 randomised communities. We then compared rankings between forests and fragments using *t*-tests.

4 | RESULTS

4.1 | Experimental release trials

4.1.1 | Wing shape

We found strong support for the hypothesis that morphological traits related to aerial movement predict flight performance. Species that successfully flew across a hostile experimental landscape had longer and pointer wings (Figure 2; Figure S1.2; Table S1.1). Likewise, mean

distance flown was positively related to residual wing length and the hand-wing index (Figure 2; Figure S1.2; Table S1.2). Significant thresholds were detected using segmented regression at -0.077 for residual wing length and 14.1 for the hand-wing index. Above these values species were largely successful at flying the full experimental distance.

4.1.2 | Wing loading

In general, species with lower wing loading flew farther (Figure 2; Table S1.3). After removing hummingbirds (family Trochilidae), which have unusually high wing loading due to unique hovering manoeuvres (Norberg, 1990) and were universally successful in completing the experimental trials, we found a significant interaction between wing loading and body mass in explaining distance flown (Figure 2; Table S1.3). Smaller species with high wing loading flew shorter distances, and this relationship eroded with increasing body mass, such that large species flew long distances despite having high wing loading. For this reason, experimental success was defined by three groups of species occupying significantly distinct components of morphospace related to wing loading and body mass (Figure 2; Table S1.3). Species most successful at crossing pasture were hummingbirds and species with extremely large body masses irrespective of wing loading, whereas unsuccessful species tended to have

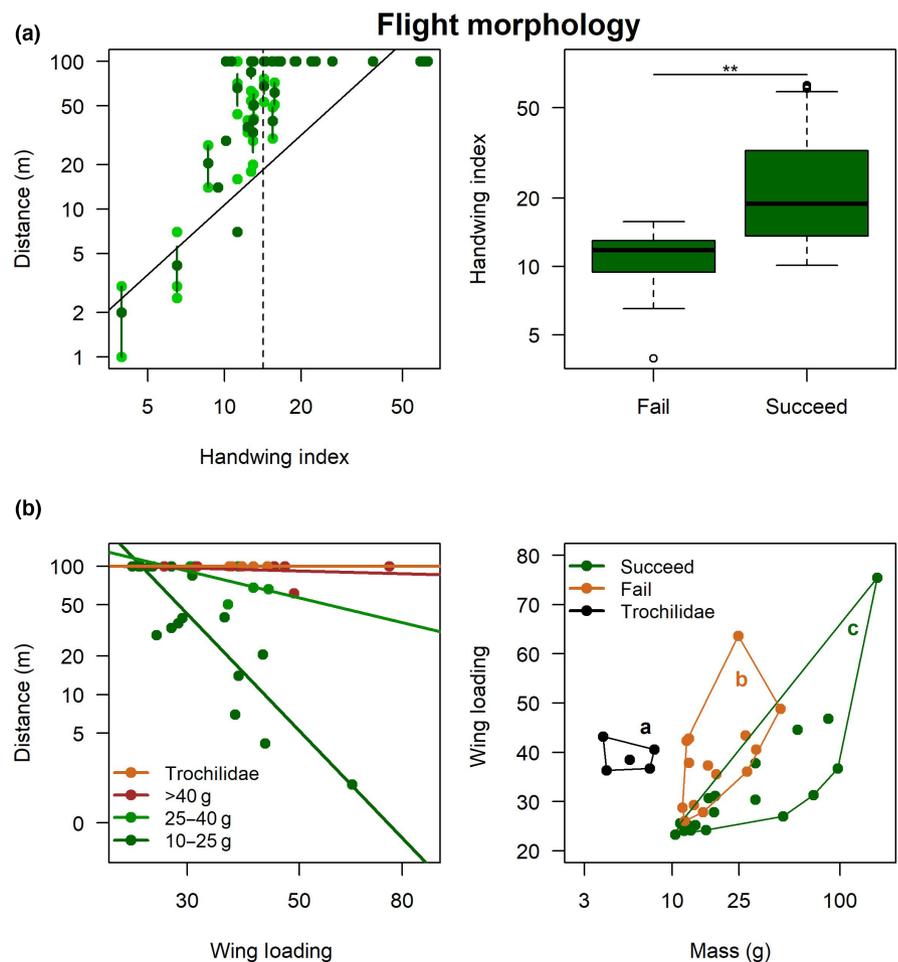


FIGURE 2 Wing morphology predicts flight performance during experimental release trials for $N=37$ species of tropical montane birds in Amazonas, Peru, 2016–2017. (a) Light green dots are individual birds, and dark green dots are species means \pm SE. The vertical dashed line indicates a morphological threshold in flight performance as quantified by segmented regression. Solid regression line and asterisks (**) indicate significant relationships ($p \leq 0.05$). (b) Interaction between wing loading and body mass explains mean distance flown. Lower cases letters define significantly different groups ($p \leq 0.05$).

smaller body masses and high wing loading. Body mass alone did not explain distance flown or success (Figure S1.2; Table S1.2).

4.1.3 | Wing shape + loading

By including the handwing index and relative wing loading in the same additive model, we quantified a continuous gradient of aerodynamic trait space defined by wing shape and mass transport (Figure 4). Species with high relative wing loading and low aspect ratio wings flew short distances compared to species with low relative wing loading and high aspect ratio wings (Table S1.5).

4.1.4 | Eye size

The avian visual system mediated flight performance, such that species with larger eyes tended to fly shorter distances (Figure 3; Table S1.2). After removing hummingbirds, which had unusually large eyes for their small body mass and were universally successful, species with larger eyes were less successful at completing the release trials (Figure 3; Table S1.1). Species with larger eyes also exhibited increased latency when leaving the release box, especially for species that waited >3s before commencing flight (Figure 3; Table S1.4).

4.1.5 | Wing + eye morphology

We found an additive effect of wing and visual morphology on flight performance, ranging from species with short-rounded wings and large eyes that flew poorly to species with longer, more pointed wings and smaller eyes that had enhanced flight capabilities (Figure 4; Table S1.5).

4.2 | Dispersal-mediated environmental filtering within fragments

4.2.1 | Fragments versus forest

In the more recently fragmented landscape of Peru (15–30 years), our results did not support predictions for the dispersal limitation hypothesis. Communities within fragments had shorter, rounder wings compared to nearby communities in otherwise similar contiguous forest (hand-wing index: $t = -3.01$, $df = 12.7$, $p = 0.01$; residual wing length: $t = -3.3$, $df = 11.0$, $p < 0.01$). There was no difference for eye size ($t = 1.02$, $df = 9.6$, $p = 0.33$; Figure 5; Figure S1.3). Similar patterns were found when controlling species richness through community randomisation (Figure S1.4). Observed community rankings were significantly lower in fragments compared to forests for the hand-wing index ($t = -2.66$, $df = 9.0$, $p = 0.02$) and residual wing

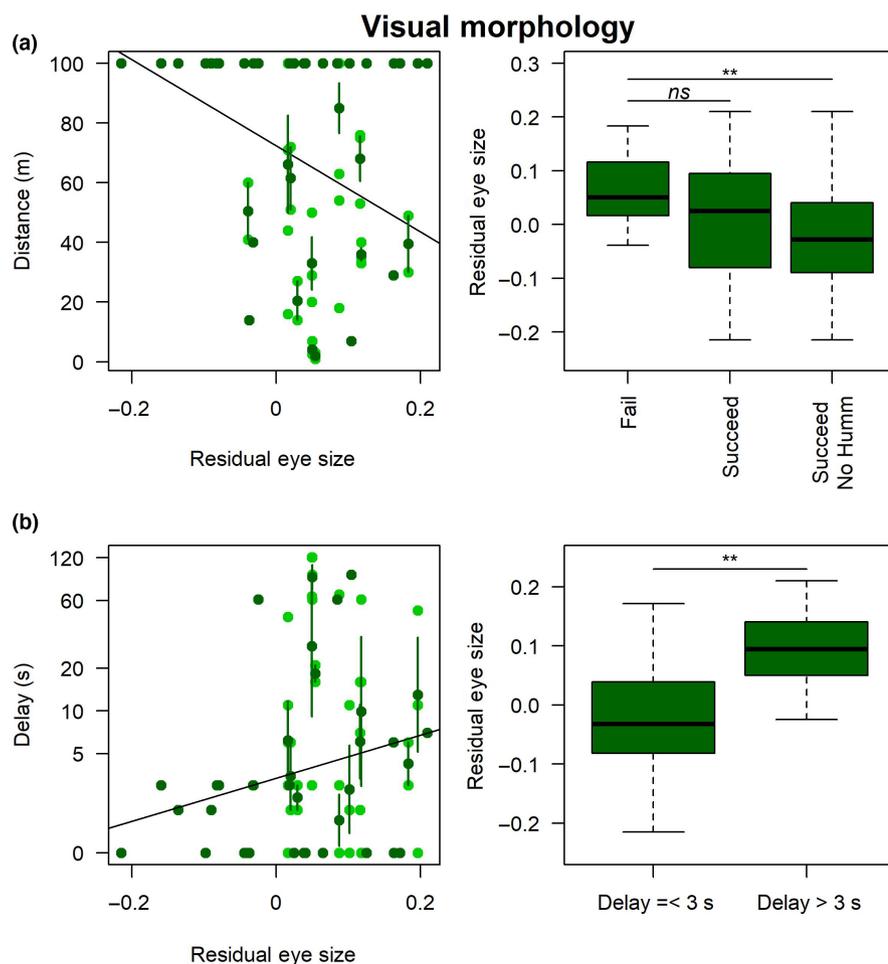


FIGURE 3 Eye morphology predicts (a) flight performance and (b) departure latency during experimental release trials for $N = 37$ species of tropical montane birds in Amazonas, Peru, 2016–2017. Light green dots are individual birds, and dark green dots are species means \pm SE. Solid regression lines and asterisks (**) indicate significant relationships ($p \leq 0.05$). Residual eye size was significantly different for successful trials when not including hummingbirds.

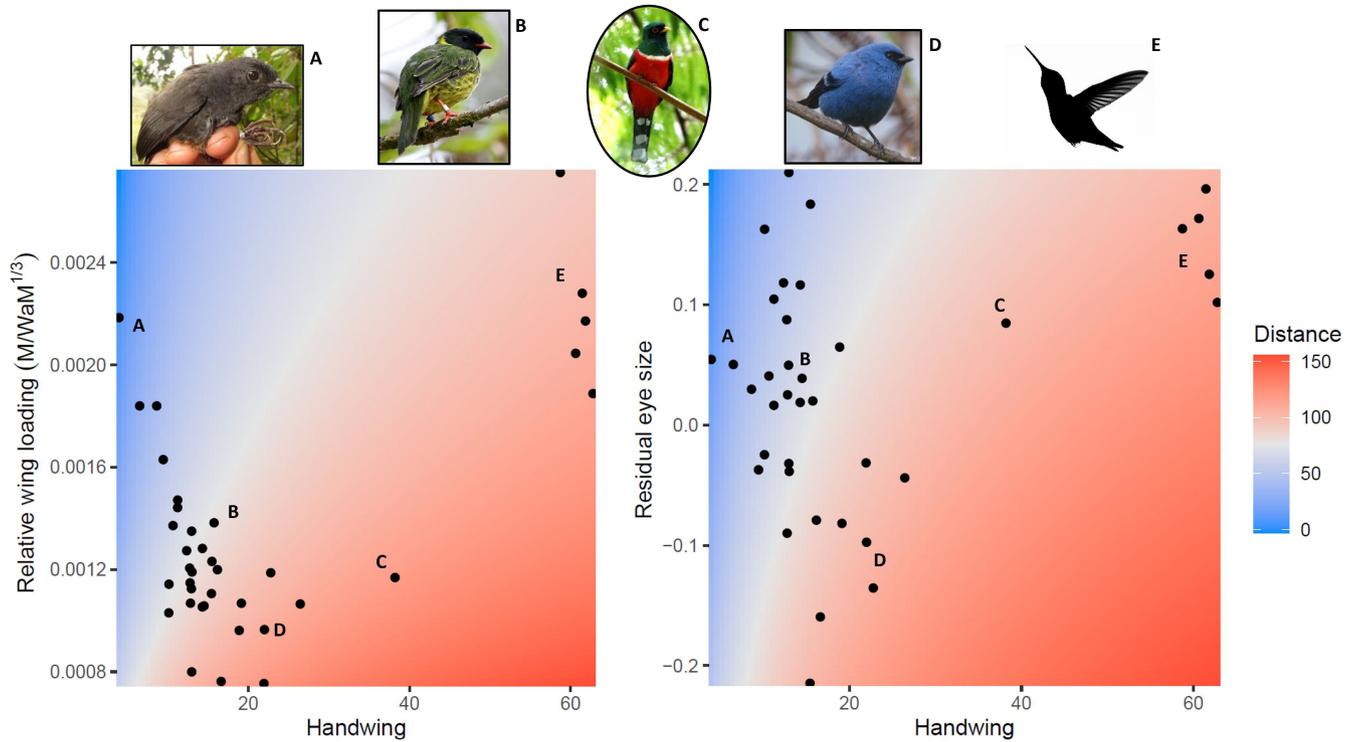


FIGURE 4 Pointed wings, low relative wing loading ($M/WaM^{1/3}$) and small eyes facilitated distance moved (m) across open pasture for $N=37$ species of tropical montane birds in Amazonas, Peru, 2016–2017. The lower righthand corner of the figure shows the projected distance a species could fly, although birds were constrained to a maximum flight distance of 100m during experimental release trials. Pictures (from top left): *Scytalopus femoralis* (I. Ausprey), *Pipreola riefferii* (IA), *Trogon personatus* (IA), *Tangara vassorii* (F. Uribe) and hummingbirds (R. Strickland).

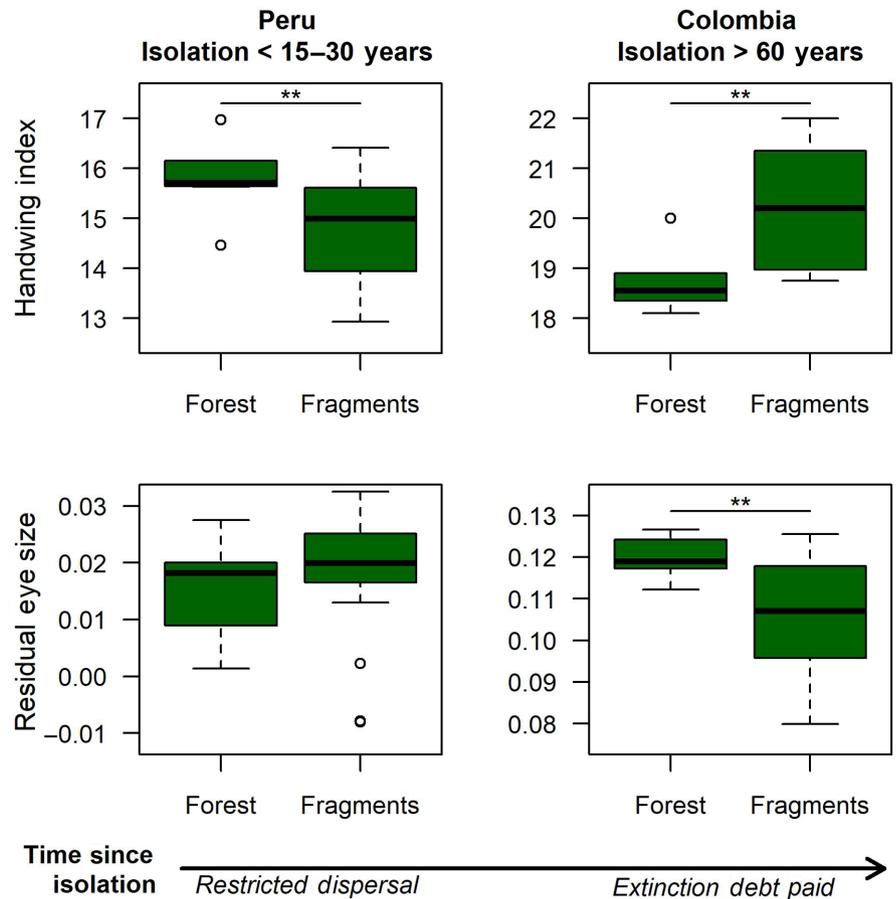


FIGURE 5 Median dispersal trait values (hand-wing index and residual eye size) for tropical montane bird communities occupying contiguous forests and fragments in Peru (recent patch isolation) and Colombia (older patch isolation). We used paired comparisons to examine relative change in trait distributions between fragments and reference forest conditions within each region. Asterisks (**) denote significant differences ($p \leq 0.05$).

length ($t = -3.3$, $df = 7.9$, $p = 0.01$), with no difference for residual eye size ($t = 0.91$, $df = 8.0$, $p = 0.39$).

In contrast, results for communities within the Colombian fragments that had been isolated longer (>60 years) were consistent with the dispersal limitation hypothesis. These communities had more pointed wings (hand-wing index: $t = 4.3$, $df = 22.0$, $p < 0.01$) and smaller eyes ($t = -3.2$, $df = 19.7$, $p < 0.01$) compared to contiguous forest communities in the same landscape. There was no difference for residual wing length ($t = -0.57$, $df = 22.0$, $p = 0.58$; Figure 5; Figure S1.3). Observed community rankings were also significantly higher in fragments compared to forests for the hand-wing index ($t = 4.9$, $df = 16.0$, $p < 0.01$) and lower for residual eye size ($t = -4.1$, $df = 21.5$, $p < 0.01$), with no difference for residual wing length ($t = 0.98$, $df = 17.7$, $p = 0.34$; Figure S1.4).

4.2.2 | Patch isolation

In Peru, the median hand-wing index of communities was negatively related to distance from forest (Figure 6; Table S1.6) and both the hand-wing index and residual wing length were positively related to the amount of matrix habitat within a 1000-m radius of each fragment (Figure 6; Table S1.6), meaning that the more isolated patches

tended to be characterised by communities with shorter and rounder wings. There was no relationship between eye size and distance from forest or amount of matrix habitat (Table S1.6).

Communities within the Colombian fragments showed the opposite pattern, with the hand-wing index being positively related to patch isolation (Figure 6; Table S1.6). Patches surrounded by the less permeable pasture matrix showed the strongest signals of dispersal-mediated filtering, with the hand-wing index being significantly higher ($\beta = 1.49$, $p < 0.01$). Distance from forest interacted with matrix type in explaining eye size variation among fragment communities ($\beta = -3.1 \times 10^{-5}$, $p = 0.03$), such that communities completely surrounded by the less permeable pasture matrix showed a negative relationship between eye size and isolation ($\beta = -1.1 \times 10^{-5}$; 95% CI: -2.02×10^{-5} , -2.24×10^{-6}), while those partially surrounded by plantations showed no relationship ($\beta = 1.94 \times 10^{-5}$; 95% CI: -5.09×10^{-6} , 4.39×10^{-5}).

5 | DISCUSSION

We demonstrate that morphological traits related to dispersal ability predict experimental flight performance, with long and pointed wings, low wing loading, and small eyes associated with improved

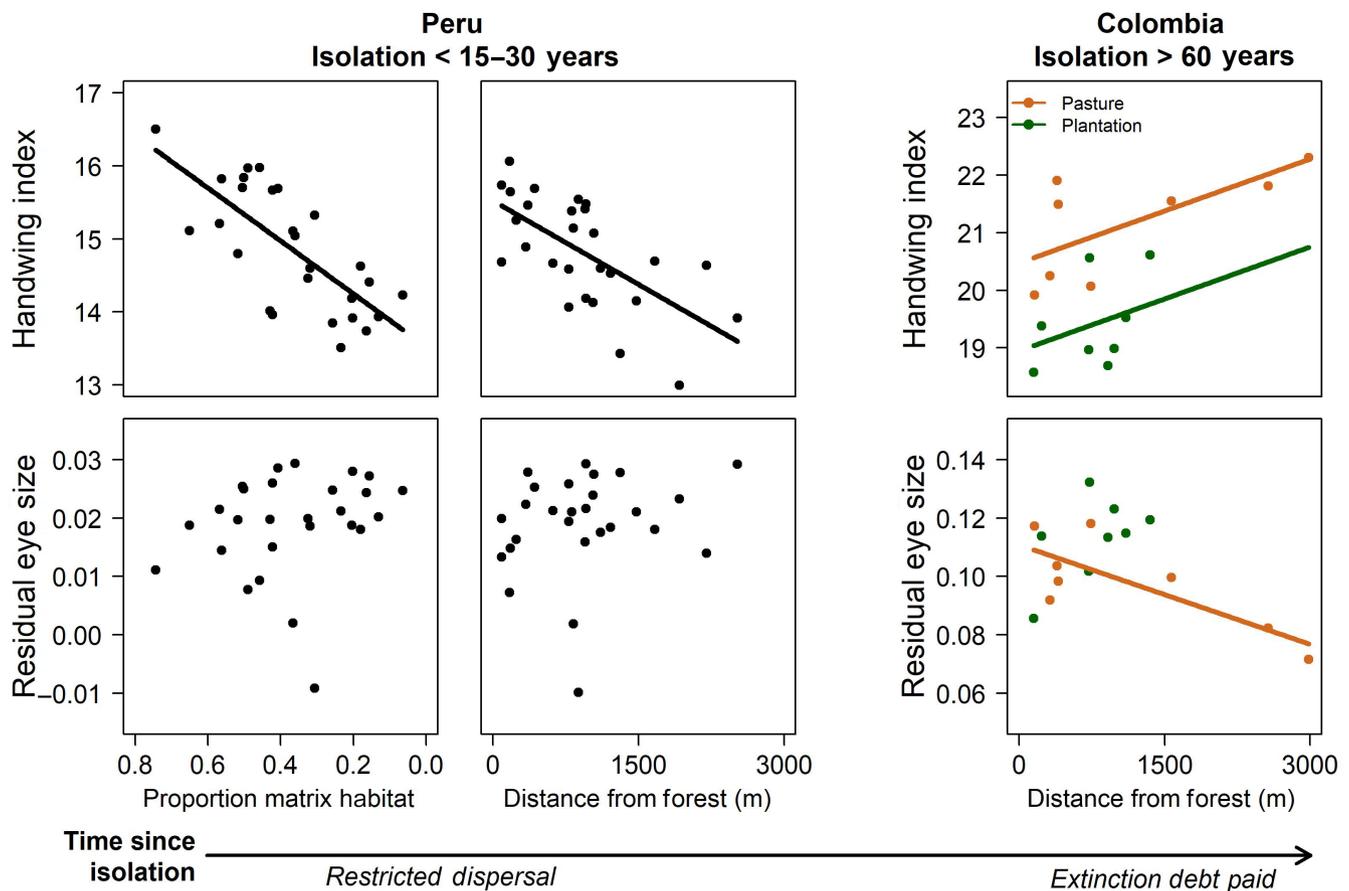


FIGURE 6 Median dispersal trait values for tropical montane bird communities in relation to patch isolation in Peru (recent isolation) and Colombia (older isolation). In Colombia, fragments were either surrounded in part by exotic tree plantations or entirely by pasture. Solid regression line indicates significant relationship ($p \leq 0.05$).

flight capacity. Furthermore, we scale these results up to the community level by showing that dispersal-mediated environmental filtering varies with the spatial and temporal aspects of patch isolation. Consistent with our original hypothesis, communities in the Colombian landscape where fragments had been isolated for longer periods of time showed predicted losses of species with poor dispersal ability, especially in fragments far from contiguous forest and in less permeable landscape matrices. However, the opposite pattern was observed in the more recently fragmented Peruvian system, suggesting that dispersal limited species not only persist in the initial period following patch isolation, but potentially accumulate due to “restricted dispersal” and represent an extinction debt yet to be paid.

5.1 | Morphological predictors of flight performance

Our results are consistent with previous experimental studies that show correlations between flight performance of tropical birds and aerial morphology (Claramunt et al., 2012; Hartfelder et al., 2020; Moore et al., 2008; Naka et al., 2022). All found that longer and more pointed wings correlate with increased flight performance, likely because wings of higher aspect ratio increase the lift to drag ratio. Furthermore, we demonstrated that the ratio of wing area to body mass (i.e. wing loading) provides additional insights related to flight efficiency beyond simple measures of wing shape (Claramunt, 2021). While small species with high wing loading were among the most flight limited (e.g. *Scytalopus femoralis* and *Drymophila striata*), large species with similarly elevated wing loading values (e.g. *Aulacorhynchus prasinus*, *Colaptes rivolii*, *Trogon personatus*) had no problem crossing the experimental landscape. Wing loading scales positively with increasing body mass, and many relatively large species with high wing loading values are highly mobile due to high aspect ratio wings that increase profile power via rapid wingbeats and, ultimately, increased flight velocities (e.g. ducks, shorebirds, and auks; Norberg, 1990, 2006). Hence, the larger species in our study may have compensated for high wing loading by being able to fly fast. Species with both high wing loading and low aspect ratio wings are particularly inefficient at taking off and maintaining slow flight, and many species with this specific trait combination (e.g. grouse) compensate with large muscle masses that generate lift via rapid acceleration (Norberg, 1990; Rayner, 1988). While we were unable to measure the muscle mass of our species, those with high wing loading and low aspect ratio consistently failed release trials (e.g. *Scytalopus femoralis*, *Drymophila striata*, *Catharus fuscater*, *Premnoplex brunnescens*, *Syndactyla rufosuperciliata*), and we assume that they possessed insufficient muscle mass to supply adequate induced power during flight (Figure 2). Collectively, results from experimental release trials corroborate evidence linking wing shape to evolutionary trajectories and large-scale movement metrics, such as natal dispersal distance or migratory propensity (Baldwin et al., 2010; Claramunt, 2021; Claramunt et al., 2012; Dawideit et al., 2009; Hartfelder et al., 2020; Kaboli

et al., 2007; Landmann & Winding, 1993; Marchetti et al., 1995; Weeks et al., 2022), and strengthens the hypothesis that wing morphology represents a key functional trait predictive of movement capacity operating across vast gradients of space and time (Sheard et al., 2020; Weeks et al., 2023).

Our results provide further support for the hypothesis that eye morphology acts as a novel dispersal trait mediating the perceptual range of species inhabiting fragmented landscapes (Lima & Zollner, 1996). The fact that species with larger eyes tended to move less easily across our experimental landscape at first appears counterintuitive given that larger eyes should provide enhanced visual acuity and the ability to better detect forest patches from longer distances (Ausprey, 2021). However, species with larger eyes tended to also delay their departure from the release box, which supports the alternative hypothesis that large eyes are maladaptive in highly disturbed landscapes due to increased glare (Fernandez-Juricic et al., 2012; Fernandez-Juricic & Tran, 2007; Martin & Katzir, 2000) and corroborates studies of tropical birds in fragmented landscapes that show large-eyed species exhibiting increased sensitivity to brightly-lit forest edges and agricultural disturbance (Ausprey et al., 2021; Jones et al., 2023; Martínez-Ortega et al., 2014).

Our results demonstrate the cumulative role that flight morphology and visual systems play in regulating experimental flight performance, and future research into physiological and microanatomical mechanisms will improve our ability to functionally predict dispersal capacity (Robinson et al., 2021). For example, heart size strongly predicts broad categories in flight behaviour, meaning that flight capacity as regulated by aerobic power may contribute to a species' ability to disperse across habitat gaps (Nespolo et al., 2018). Likewise, studies that quantify interspecific variation in key aspects of muscle physiology that regulate flight performance, such as myoglobin concentration, fatigue resistance, and the extent of different myosin isoforms, are particularly needed (Condell et al., 2022; Robinson et al., 2021). In terms of avian visual systems, the role of retinal cell specialisation and colour recognition in regulating movement behaviour in fragmented landscapes remains unknown. Avian retinal cell ganglia (RCG) contain specialised visual pigments and oil droplets that maximise colour recognition at different light wavelengths and are thought to correspond to the ambient spectral environments found in habitats frequented by a given species (Hart, 2001). Hence, studies that combine metrics for both visual sensitivity (such as eye size, focal length, or RCG specialisation) and colour recognition will make importance contributions toward predicting interspecific variation in dispersal capacity and sensitivity to fragmentation (Moore et al., 2017; Stratford & Robinson, 2005; Thomas et al., 2004).

5.2 | Aerodynamic thresholds and dispersal limitation

Our results from the experimental release trials revealed a threshold in flight capacity beyond which species were reliably able to cross

the experimental landscape (hand-wing index >14). This is remarkably similar to a threshold predicting speciation rates within the family Furnariidae. In this case speciation rates rapidly increased for species with hand-wing index <15, likely due to isolation caused by extreme dispersal limitation (Claramunt et al., 2012). This suggests that an aerodynamic threshold exists for the role of flight in driving both community assembly and evolutionary trajectories and calls for future research into the specific flight mechanics underlying dispersal limitation across ecological and evolutionary time scales.

5.3 | Dispersal-mediated environmental filtering in isolated fragments

Our results suggest that the spatial and temporal dimensions of patch isolation act as dispersal-mediated environmental filters for bird communities persisting in fragments, with communities existing along a continuum of extinction debt (Halley et al., 2016). Results from the Colombian landscape where fragments had been isolated >60 years support the hypothesis that extreme temporal and spatial isolation leads to highly filtered dispersal traits. Community trait values for the hand-wing index were higher than those in nearby contiguous forests, indicating a loss of forest specialists with short-rounded wings and limited flight ability (e.g. *Drymophila caudata*, *Cyphorhinus thoracicus*, *Grallaria alleni*, *Pipreola riefferii*) and colonisation by habitat generalists with enhanced dispersal ability (e.g. *Tyrannus melancholicus*, *Turdus ignobilis*, *Thraupis episcopus*; Gómez et al., 2021; Renjifo, 2001). In this sense, fragmentation over the long-term filtered for species with an improved lift to drag ratio and lower induced power requirements and associated energetic costs when navigating among habitat patches (Norberg, 1990). Furthermore, species with improved flight efficiency and visual adaptations to glare associated with brightly lit agricultural matrices were more likely to persist in patches with extreme spatial isolation. In this case, the filtering of dispersal traits intensified in fragments far from source populations in contiguous forests, especially when surrounded by a hostile landscape matrix that offered limited patch connectivity.

In contrast, we observed the opposite pattern in the more recently fragmented landscapes in Peru (15–30 years post-isolation). Here, communities in fragments had short, rounded wings compared to nearby forests and larger eyes, especially for fragments farther from contiguous forest and surrounded by less permeable matrix habitat. We suggest that this pattern occurs due to a phenomenon we term “restricted dispersal”, in which dispersal-limited species are effectively “trapped” within fragments during the initial years following patch isolation. This hypothesis is supported by prior analyses at the same sites in which the abundance of many species with shorter-rounded wings increased in fragments compared to forest, pointing toward an “accumulation” of individuals restricted by isolation (e.g. *Conopophaga castaneiceps*, *Scytalopus femoralis*, *Syndactyla rufosuperciliata*, *Arremon brunneinucha*, *Thamnophilus caerulescens*, and *Grallaricula ferruginepectus*; Ausprey et al., 2022, 2023a). This phenomenon has also been

observed in highly isolated fragments of rainforest in Costa Rica where the dispersal-limited *Poliocrania exsul* occurs at high density and displays early signs of inbreeding (Visco & Sherry, 2015; Woltmann et al., 2012). The Peru fragments may also have been experiencing a form of “colonization debt”, in which matrix species with enhanced dispersal ability had yet to settle, a process documented to progress over multiple decades following patch isolation (Gómez et al., 2021). Given that tropical birds have lifespans >10 years (Scholer et al., 2018), dispersal-limited species could persist indefinitely in the absence of immigration if adult survival and population growth rates remained sufficiently high (Semper-Pascual et al., 2021). This seems unlikely, however, given that demographic studies of tropical birds in fragments point to population collapse, especially in small, highly isolated patches (Korfanta et al., 2012), suggesting that communities in the more recently isolated Peruvian fragments owe an extinction debt yet to be paid.

6 | CONCLUSIONS

The generalisation of our results at a global scale likely depends upon the range of dispersal traits displayed by regional species pools. Both the hand-wing index and residual eye size vary with latitude, with tropical bird communities composed of more species with short-rounded wings and larger eyes (Ausprey, 2021; Sheard et al., 2020), and global analyses show a latitudinal gradient in edge sensitivity as mediated by dispersal ability that peaks in the Tropics (Weeks et al., 2023). This supports hypotheses long-held by ornithologists that tropical birds are especially dispersal limited due to reduced flight capacity and preference for dark forest interiors with limited environmental disturbance (Stratford & Robinson, 2005; Wallace, 1889; Willis, 1974). Temperate bird communities include many migratory species that are likely less susceptible to dispersal-mediated environmental filtering and likely lack many species with both high wing loading and low aspect ratio. Additional field studies across different regional bird communities will further elucidate the generalisability of trait-mediated dispersal limitation in driving avian community disassembly in fragmented landscapes throughout the world.

AUTHOR CONTRIBUTIONS

Ian J. Ausprey conceived the ideas, analysed the data and led the writing of the manuscript. Ian J. Ausprey and Felicity L. Newell designed the methodology and collected the data. All authors contributed critically to the drafts, provided funding and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.83bk3j9zg> (Ausprey et al., 2023b).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix 1. Supplementary Tables and Figures.

Appendix 2. Vegetation structure of contiguous forest and fragments in Peru and Colombia.

Appendix 3. Project Collaborators in Peru.

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