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Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds

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Variation in species richness across environmental gradients may be associated with an expanded volume or increased packing of ecological niche space. However, the relative importance of these alternative scenarios remains unknown, largely because standardized information on functional traits and their ecological relevance is lacking for major diversity gradients. Here, we combine data on morphological and ecological traits for 523 species of passerine birds distributed across an Andes-to-Amazon elevation gradient. We show that morphological traits capture substantial variation in species dietary (75%) and foraging niches (60%) when multiple independent trait dimensions are considered. Having established these relationships, we show that the 14-fold increase in species richness towards the lowlands is associated with both an increased volume and density of functional trait space. However, we find that increases in volume contribute little to changes in richness, with most (78%) lowland species occurring within the range of trait space occupied at high elevations. Taken together, our results suggest that high species richness is mainly associated with a denser occupation of functional trait space, implying an increased specialization or overlap of ecological niches, and supporting the view that niche packing is the dominant trend underlying gradients of increasing biodiversity towards the lowland tropics.

1. Introduction

Latitudinal and elevational gradients in diversity are widespread across the tree of life, with species richness in most groups declining from the tropics to the poles and from low to high elevations [1,2]. Despite the generality of these patterns, the underlying mechanisms are poorly understood [3–5]. Geographical gradients in richness may to some extent be explained by historical factors, particularly variation in the rate or time available for species diversification, yet they are also likely to reflect deterministic differences in the ecological capacity of environments to support diversity [3]. Macarthur [6] argued that gradients in richness could be associated with at least two contrasting patterns of niche occupancy. According to the 'niche expansion' model, increases in richness are associated with the occupation of novel regions of niche space (i.e. habitat and resource dimensions), which are either unavailable or have yet to be exploited by more depauperate assemblages [6,7] (figure 1a). An alternative view—the 'niche packing' model—proposes that higher diversity is instead associated with the denser packing of niche space (figure 1b). This could arise either through finer specialization or greater overlap in resource use [7,8], which in turn may reflect differences in the ecological capacity for coexistence or regional differences in rates of species production [6,9]. These models of niche packing and expansion are not mutually
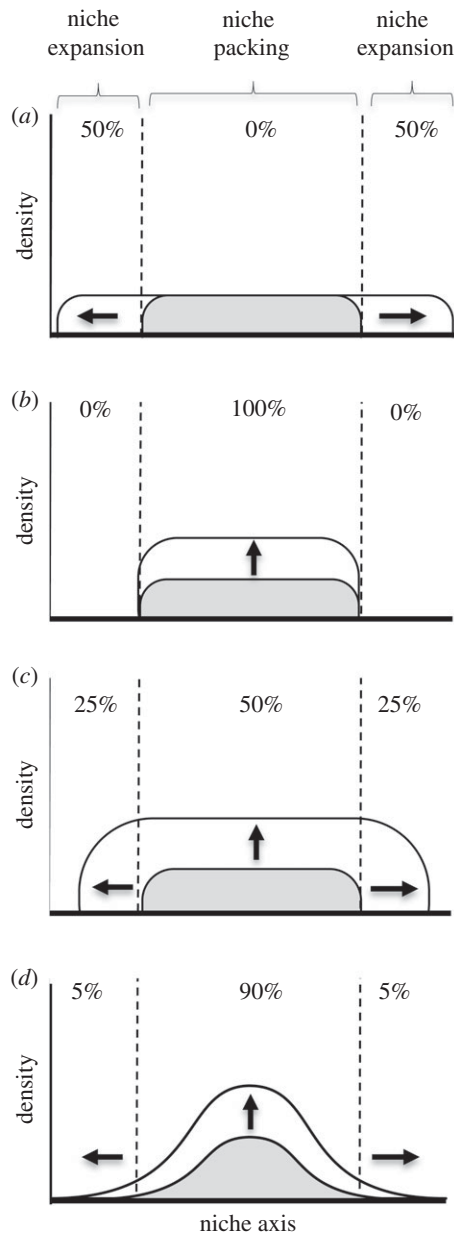
Figure 1. Three conceptual models of increasing niche density and volume, comparing assemblages of low (shaded) and high (white) species richness. The niche expansion model (*a*) predicts that increases in richness are associated with an expanding niche space (increasing volume), whereas the niche packing model (*b*) predicts that increasing richness is associated with greater niche packing (increasing density) arising though either greater specialization or overlap in resource use. In a combined model, whereby increases in assemblage richness are accommodated through both niche expansion and packing, their relative contribution depends on the distribution of species within trait space (*c,d*).

exclusive and both may occur in tandem (figure 1*c,d*). However, the relative extent to which major gradients in richness are associated with an increased volume or packing of niche space remains disputed [4,5,10].

The greater phenotypic variety of life in the tropics has long inspired the idea that global patterns of richness are shaped by latitudinal gradients in the volume of available niche space [6,11]. Accordingly, several analyses have confirmed that the richness of consumers is often tightly correlated with the richness or ecological diversity at lower trophic levels [4,11,12]. In contrast, the extent to which niche packing changes along diversity gradients is more contentious, not least because the

underlying relationships are complex and difficult to measure [4,5]. One approach to addressing this question is to classify species into functional groups (e.g. based on diet, behaviour and life history) and then examine how the number of functional groups changes with richness [13–15]. While studies using this technique generally show that more speciose communities consist of more densely packed [14,15] and specialized guilds [13], this may be a methodological artefact given that studies using more detailed and quantitative data on resource use have generated mixed results [4,5], producing evidence that increased richness is associated with higher [10,16], unchanged [17] or even lower levels of specialization [18].

An alternative approach is to quantify the morphological trait space (hereafter termed 'morphospace') occupied by assemblages [7,19]. This trait-based approach provides a potentially powerful tool for testing geographical gradients in niche structure because it does not require subjective decisions regarding the scale and classification of species into ecological guilds. However, because information on phenotypic traits is rarely available across sufficiently large taxonomic and geographical scales, such analyses have been undertaken in only a few specific systems [20–24]. Furthermore, this approach may depend critically on the choice of morphological traits, and while these are typically selected on the basis of their presumed ecological importance, previous studies have not explicitly tested the underlying assumption that morphological traits are truly functional, reflecting adaptations to the ecological niche [25]. Thus, there has been surprisingly little progress in understanding how the density and volume of niche space changes across broad-scale diversity gradients, or whether this question can be adequately tackled by quantifying species functional traits.

To address these issues, we compiled a dataset of morphological and ecological traits for 523 resident species of passerine birds (Aves: Passeriformes) distributed across a single elevation transect in the Andes of southern Peru. This transect spans from species-poor puna grasslands at the Andean snowline (4000 m elevation) to the lowland forests of Amazonia (250 m) where over 300 resident species (breeding locally) have been recorded within a 100-ha plot [26]— the highest avian alpha-diversity recorded worldwide. The Andes-to-Amazon slope in this region supports approximately 10% of the world's passerine bird species and has provided a classic system for examining diversity gradients since the seminal studies of Terborgh [27,28]. In addition to its extremely high diversity, the system is ideal for macroecological tests because detailed information is available on the local occurrence and elevational distributions of all species [29]. Moreover, unlike most elevational transects [30], it is largely free from human disturbance, and thus offers a unique insight into natural patterns of biodiversity prior to significant modification by land-use change [23,28].

This study has two key aims. First, we investigate the correspondence between morphological traits and major dimensions of passerine niche space represented by key dietary and foraging guilds. While a number of studies have reported a relationship between morphological traits and ecological niches in birds [25,31,32], previous tests have focused on relatively few species, mainly in the temperate zone. Second, having established these relationships in our system, we assess how the structure of passerine morphospace changes with elevation. To do this, we use data from across passerines and within individual ecological guilds to examine gradients in

the volume and density of morphospace, hereafter termed 'morphovolume' and 'morphodensity', respectively. We then quantify the extent to which increasing richness is associated with an expansion in the total bounds (figure 1a) or increased internal packing of trait space (figure 1b). Finally, we explore the underlying basis of changes in trait packing by testing how specialization in species dietary and foraging niches varies across the elevational gradient.

2. Material and methods

(a) Elevation data

Field surveys conducted over several decades have provided a comprehensive list of resident and non-resident species ($n = 1006$) occurring in Manu National Park, Peru, with estimates of upper and lower elevation range limits to 50 m resolution [29]. For clarity, we refer to each 50-m elevational band by its uppermost elevation, e.g. 4000 m indicates the elevational band spanning from 3950 to 4000 m. We focused on year-round resident passerines, excluding species that are migratory or occur only as vagrants ($n = 50$). We generated species assemblages occurring within each 50 m band by interpolating between lower and upper range limits. The tendency of this method to inflate richness at mid-elevations does not pose a significant problem for our analysis because almost all species on the Manu slope occupy a single continuous elevational zone, often increasing in abundance towards its centre [28]. Richness estimates of elevational bands (i.e. gamma diversity) may be biased by differences in spatial area, and thus beta-diversity [33]. To minimize area effects, we limited our analysis to species locally surveyed (i.e. alpha-diversity) along a single transect [33], the Kosnipata valley ('Manu Road'), which has been the focus of intensive sampling at all elevations. Our final dataset contained 523 species (electronic supplementary material, database S1).

(b) Morphological traits

We collected morphometric measurements from live birds mist-netted at the study location in 2010 ($n = 2006$ individuals of 222 species; see [34]), and from preserved museum skins ($n = 2203$ specimens of 467 species) (see electronic supplementary material, database S1, for list of contributing institutions). The seven traits measured (to the nearest 0.01 mm) were beak length, width and depth, tarsus length, Kipp's distance, wing length and tail length (see electronic supplementary material, table S1, for further descriptions). We selected these traits because of their presumed association with important dimensions of the avian niche (e.g. [25,31]). Where possible, we obtained measurements from at least four individuals (two from each sex; mean total = 8 individuals) per species (we excluded three species for which biometric data were incomplete).

Based on the covariance matrix of species mean trait values (log-transformed), we constructed a seven-dimensional morphospace using principal component (PC) scores. The use of mean scores is appropriate because most of the variance in traits occurs among rather than within species (median across traits = 95%; electronic supplementary material, table S1). The first three PC axes together accounted for 90% of the variation in species trait values (electronic supplementary material, table S2). Correlations with the original morphological variables indicate that these axes represent overall body size (PC1), the ratio of Kipp's distance to tarsus length and bill size (PC2) and the ratio of tail length to beak width and depth (PC3) (see electronic supplementary material, table S2, for PC loadings). Despite accounting for little variation in traits, additional dimensions (PC4–7) may have important roles in defining avian niche space [25]. We therefore retained all seven axes in our analyses, with PC scores normalized to have a mean = 0 and s.d. = 1 (for further justification see below and the electronic supplementary material).

(c) Ecological guilds

We used recently published data [35] on the proportional use of different food types to classify species into four dietary guilds: specialist insectivore, granivore or frugivore (i.e. more than or equal to 60% food obtained from corresponding food type) and omnivores (i.e. less than 60% food obtained from any single food type). Most study species (68%) were specialist insectivores, so to provide finer-scale information about behavioural or micro-habitat components of the niche for this component of passerine diversity, we scored the proportional use of different foraging attack strategies: aerial screen, ground pick, aerial attack, perch glean, branch probe and dead-leaf probe (from 0 to 100% in 10% increments). Finally, for the most speciose attack categories, 'aerial attack' and 'perch glean', we further subdivided scores according to the specific substrate from which prey is obtained: air, ground, foliage and branch. In summary, we scored each species according to 14 ecological guild categories distributed across three hierarchical (nested) levels: (i) diet (four classes, $n = 520$), (ii) insectivore foraging manoeuvre (six classes, $n = 355$), and (iii) foraging substrate (four classes, $n = 302$). Further description of ecological guilds and a summary of the protocol are provided in the electronic supplementary material, figure S1 and table S3).

(d) The relationship between morphology and ecology

To test the relationship between morphology and ecology, we stochastically assigned species to guilds with a probability based on their observed guild membership scores, repeating this 100 times. For each of these replicate assignments, we then tested whether morphological traits predict membership of guilds using a random forest model (see electronic supplementary material). This machine learning approach grows an ensemble of classification trees (500) based on bootstrapped samples of the original data and provides an unbiased estimate of predictive ability as the percentage of the remaining 'out of bag' species classified to the correct guild. Throughout, we report the mean classification accuracy for each of the three hierarchical guild categories (diet, foraging manoeuvre and foraging substrate).

The use of normalized PC trait axes when quantifying assemblage morphospace assumes that each trait axis is of similar importance in charactering avian niche space [36,37]. To test this assumption, we estimated the contribution of each PC trait in predicting guilds by removing each axis as a term from the model and calculating the drop in classification accuracy. Finally, we examined the possibility that we had missed potentially important trait axes from our analysis by calculating how classification accuracy increases with the number of raw morphological traits (i.e. from one to seven traits) used to construct passerine morphospace (see the electronic supplementary material).

(e) Morphovolume and morphodensity

Because our classification analysis revealed that many trait axes are required to describe niche space, we calculated morphospace structure based on all seven PC axes. For each assemblage, we quantified morphodensity using the mean Euclidian distance between nearest neighbours in trait space (MNND) [19] and morphovolume using the minimum convex polygon (MCPV) [38] implemented in the R package 'geometry' (MCPV was only calculated for assemblages containing seven or more species). We note that the gradient in morphovolume was robust to the potential bias in estimates introduced when applying the MCPV to assemblages containing few species [39] (see the electronic supplementary material). As an alternative metric of

morphospace structure, we calculated the sum of the variances across PC axes (VAR) [40]. In contrast to MNND and MCPV, this index is expected to be independent of richness and is sensitive to changes in both density and volume, thus providing an indication of the relative strength of these two patterns.

A limit to the phenotypic similarity of coexisting species is expected to lead to a more even packing of species within morphospace [40]. For each assemblage, we calculated the functional evenness index (FEve) [39], quantifying the regularity of branch lengths in the minimum spanning tree connecting species in multivariate trait space. FEve varies from 0 to 1 for assemblages with low and high evenness, respectively. Finally, to examine how species are distributed throughout functional trait space, we quantified the density of species within concentric spherical shells spaced at intervals of 1 s.d. from the centroid or morphospace [37].

Even if species were distributed across elevation independently of their traits, gradients in morphospace structure may still arise by chance. For metrics that are sensitive to richness (MNND and MCPV), we additionally want to know whether observed gradients in morphospace depart from those expected given the gradient in species richness. We thus compared the observed gradient in each metric to that expected under a null model in which PC trait scores were randomly permuted across all species on the gradient ($n = 500$ replicates). This approach was preferred to randomizing species elevation distributions because it maintained the observed patterns of richness and range contiguity. We repeated this analysis separately within individual guilds and six large avian families (Cotingidae, Dendrocolaptidae, Thamnophilidae, Thraupidae, Tyrannidae and Furnariidae).

Our analysis allows us to test how the structure of morphospace changes across the elevation gradient, but does not directly quantify the relative contribution of trait packing and expansion to changes in richness [24]. For instance, a given expansion in morphovolume can be associated with either a substantial (figure 1c) or marginal (figure 1d) increase in richness, depending on the distribution of species within trait space. Based on the idea that niche expansion corresponds to the extension of niche axes [6,11], we quantified niche packing as the % of the additional species in the more diverse lowland assemblage (A_1) occurring within the volume of multivariate trait space occupied by the more depauperate highland assemblage (A_2). The most basic metric of niche packing is simply the % of the additional species in A_1 enclosed within the MCP of A_2. However, this approach assumes that the structure of trait space remains constant across the gradient and may thus be confounded by changes in the shape or position of morphospace (see the electronic supplementary material). To overcome this problem, we developed a greedy search algorithm to calculate the % of species in A_1 that could be contained within a MCP of volume equivalent to A_2, but where the position and shape of morphospace was not constrained (see the electronic supplementary material for details). Using this approach, we quantified niche packing in two different ways. First, we compared packing between adjacent elevation bands. For this analysis, we used bands of 200 m thickness to ensure a sufficient number of species were added to each assemblages to provide a reliable estimate of packing. Second, we quantified packing between the most diverse lowland assemblage and selected assemblages at mid- and high elevations. We repeated this separately for each of the three most diverse avian guilds on the gradient (insectivores, frugivores and omnivores). In each case, elevational bands were selected to represent a successive doubling in species richness. For instance, across passerines in total, assemblages were located at 3250 m ($n = 70$), 1600 m ($n = 144$) and 300 m ($n = 286$) (elevations are provided in electronic supplementary material, table S4). Using these focal assemblages, we partitioned the additional species at lower elevations into components arising from either the packing or expansion of the morphovolume occupied at higher elevations.

(f) Ecological specialization

We tested how ecological specialization varies across the elevation gradient using the guild categories (diet, insectivore foraging manoeuvre and gleaning/aerial attack substrate) to calculate specialization (S) with the Levins' index [41],

$$S = \frac{1}{\Sigma pi^2},$$

where pi is the proportional use of category i, and lower scores indicate greater specialization. We used this index to assign species as 'specialists' ($S = 1$) or 'non-specialists' ($S > 1$) and, treating this as a binary trait, tested the relationship with species mid-point elevation range in a generalized linear model. We did not use raw S scores because these were strongly right skewed and transformations failed to improve the normality of model residuals (electronic supplementary material, figure S2). We repeated our analysis accounting for species non-independence due to shared ancestry by including the phylogenetic covariance between species as a random effect (see the electronic supplementary material).

3. Results

(a) The relationship between morphology and ecology

We found that different avian guilds map onto different regions of morphospace in expected ways (electronic supplementary material, figures S3–S5 and table S5). For instance, species that screen insects from the air (e.g. swallows, Hirundinidae) have long, pointed wings relative to their body size, occupying extreme positions along PC2 and PC7 (electronic supplementary material, figures S3 and S5). In contrast, species that probe insects from branches and tree trunks (e.g. red-billed scythebill, *Campylorhamphus trochilirostris*) have relatively large bodies and long bills, occupying extreme positions along PC1 and PC4 (electronic supplementary material, figure S3). Our random forest model showed that for specialist dietary guilds, 67–76% of species can be assigned to the correct class based on their morphological traits. In contrast, classification accuracy was—as expected— lower for omnivores (45%) (electronic supplementary material, table S5 and figure S4). Within insectivores, the same traits are also informative, allowing classification of species to the correct guild with a high degree of accuracy (e.g. aerial screen, 95%; aerial attack, 71%; and ground pick, 78%) (electronic supplementary material, table S5 and figure S4). Classification accuracy is more limited for species obtaining prey from foliage and branches (gleaning, 41%; probing, 51%) and precise substrate use was only weakly predictable (42–62%) (electronic supplementary material, table S5 and figure S4). In all cases, classification accuracy increases with both the number of measured traits and PC axes used to construct morphospace (electronic supplementary material, figure S4). Importantly, we find that each individual PC axis has a similarly low contribution to classification accuracy (electronic supplementary material, table S6) that is independent of the amount of variance accounted for in the original morphological traits (electronic supplementary material, table S2). Together, these results justify the use of both normalized trait values and the retention of all PC axes when calculating morphovolume and morphodensity (see the electronic supplementary material).
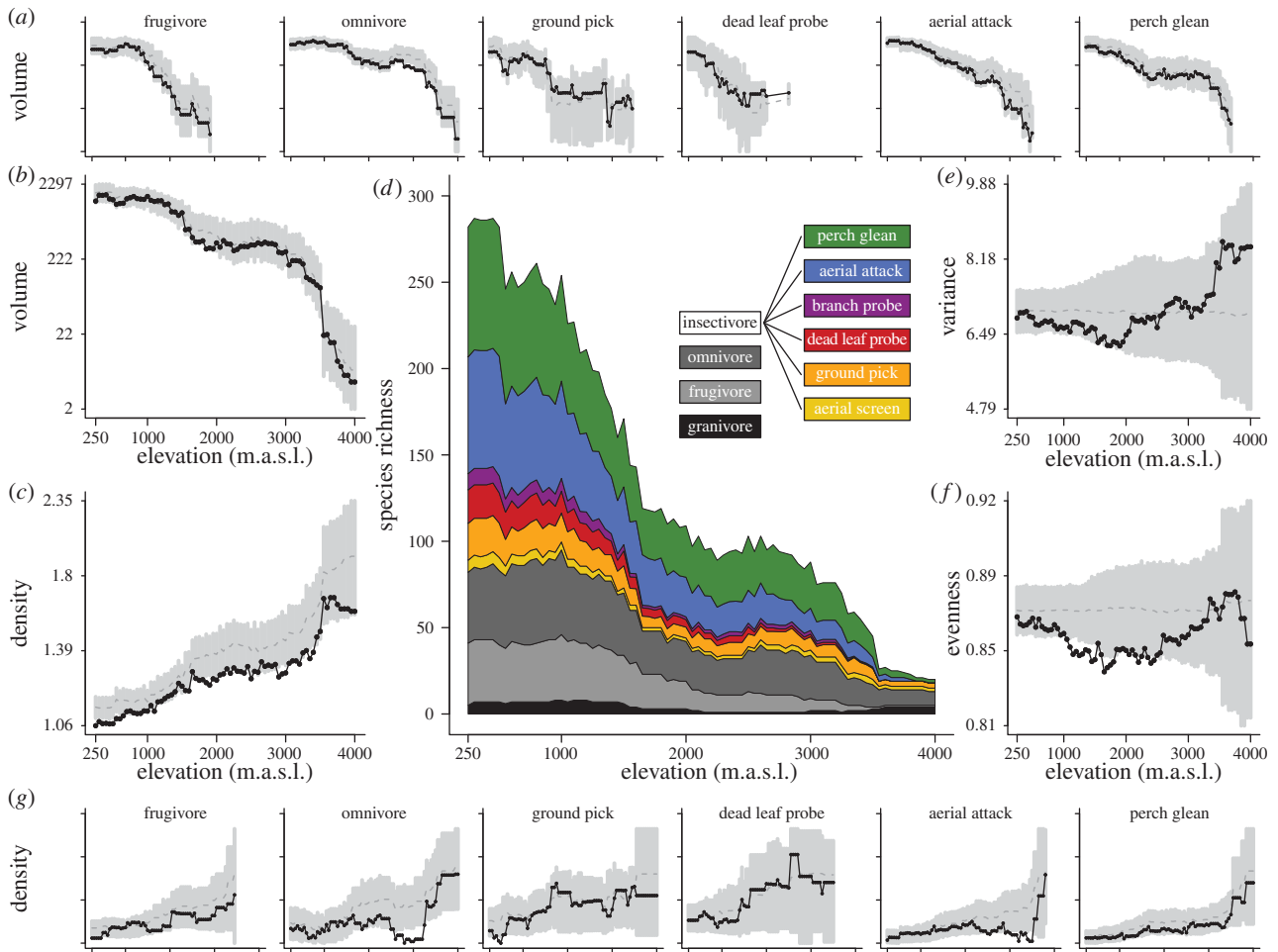
Figure 2. The Andes–Amazon elevational gradient in assemblage richness and the structure of functional trait space across passerines and ecological guilds. (a) The volume of morphospace (MCPV) occupied by individual guilds (results are shown for the six most speciose guilds); (b) the volume and (c) density of morphospace (MNND) across passerines; (d) the gradient in species richness and contribution of each ecological guild; (e) the variance in trait values (VAR) and (f) evenness (FEve) of trait spacing across passerines and (g) the density of morphospace within individual guilds. Grey bars (a–c, e–g) show the expected (95% CI) value for each morphospace metric under the null model.

(b) Gradients in species richness, morphovolume and morphodensity

Passerine richness increases monotonically with decreasing elevation, from 21 species in the highlands (4000 m) to a maximum of 286 species in the lowlands (300 m) (figure 2d). All guilds are represented at even the highest elevations (i.e. greater than 3500 m) and thus the gradient in richness is entirely driven by increases in richness within guilds (figure 2d). However, increases in richness are not partitioned equally across guilds, with some barely increasing in richness (e.g. granivores) and others increasing dramatically (e.g. insectivores that 'perch glean' or 'aerial attack') (figure 2d).

As richness increases towards low elevations, there is a continuous expansion in morphospace volume, as quantified using the MCPV (figure 2b). Increasing richness towards the lowlands is also accompanied by increasing morphodensity, as indicated by a decrease in nearest neighbour distances (MNND) (figure 2c). Across elevations, assemblage morphovolume was consistent with that expected under the null model in which the position of species in trait space is independent of elevation (figure 2b). In contrast, MNND were consistently smaller than null model expectations, although there was little evidence to suggest that MNND declined towards the lowlands faster than expected given the observed gradient in richness (figure 2c). In contrast to the monotonic gradient in MCPV and MNND, both the

variance in assemblage trait values (figure 2e) and functional evenness (figure 2f) exhibit a distinct two-phase relationship with elevation, initially declining from the highlands (greater than 3500 m) to mid-elevations (1500–2000 m), before subsequently increasing towards the lowlands (less than 500 m). Although we could not reject the null model when explaining changes in VAR (figure 2e), the gradient in FEve departed significantly from random, with mid-elevation assemblages less evenly packed than expected by chance (figure 2f).

An expansion in morphovolume and increase in morphodensity towards the lowlands was also evident within guilds (figure 2a,g; electronic supplementary material, figure S6) and avian families (electronic supplementary material, figure S7). However, for omnivores, as well as insectivores using 'aerial attack', the gradient in MNND was more complicated, with the highest morphodensity occurring both in the lowlands and in a zone centred around 3000 m (figure 2g). This high elevation peak in morphodensity departed from null model expectations and was driven by the dominance in these assemblages of a single clade, the Tyrannidae, which, in contrast to other large families, exhibited small MNND across all elevations despite continuously increasing richness towards the lowlands (electronic supplementary material, figure S7).

Across much of the elevational gradient, morphovolume and morphodensity increase at a rate that is largely consistent
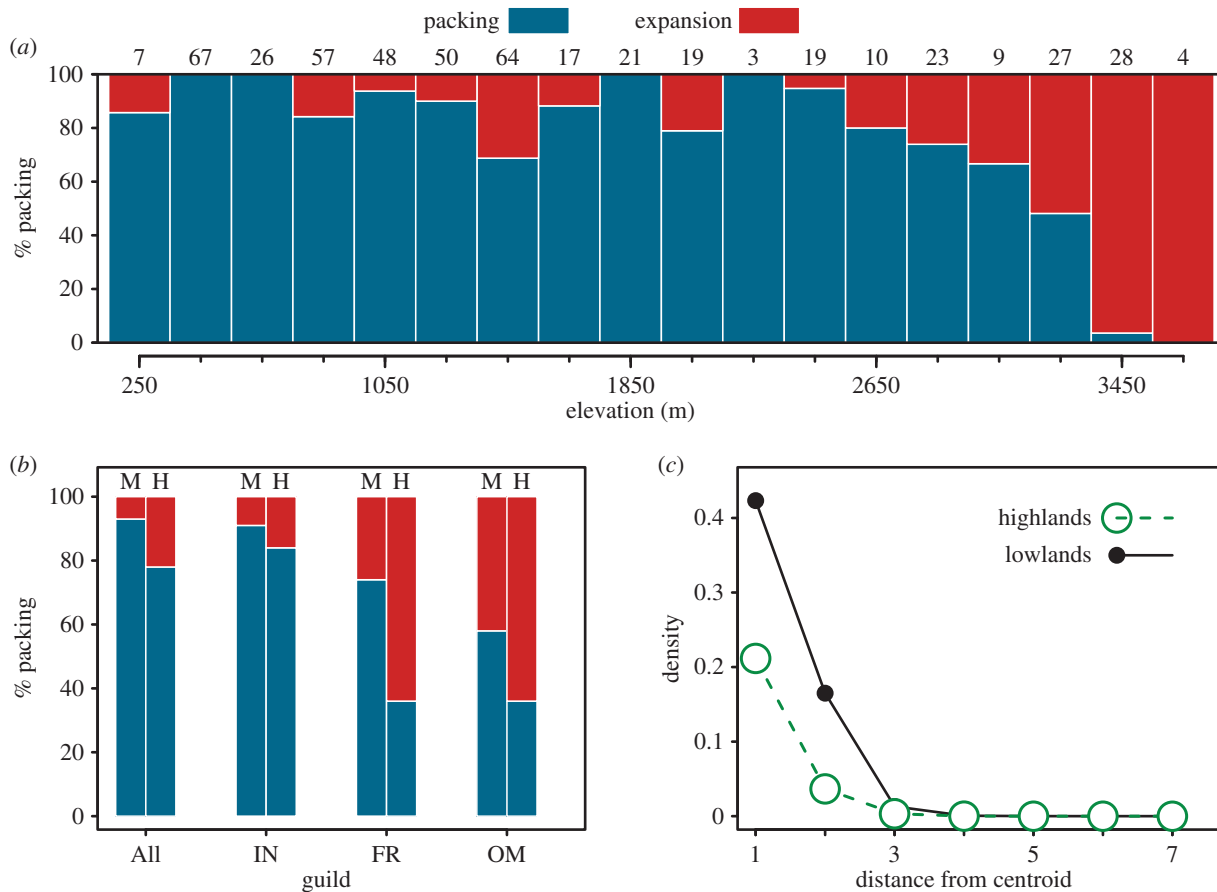
Figure 3. Niche packing and expansion in passerine birds distributed across the Andes – Amazon elevational gradient. The % contribution of niche packing (blue) versus expansion (red) to (a) total passerine richness between adjacent elevation bands, and (b) between the lowlands, mid-elevations (M) and highlands (H). In (a), the morphovolume of additional species in each band is compared with the single adjacent higher elevation band; numbers above bars show sample sizes. In (b), the % contribution of niche packing across the gradient is shown separately for all passerines ('All') and within the most diverse guilds (IN, insectivore; FR, frugivore; OM, omnivore). In (c), the morphodensity (the density of species within passerine morphospace) in the lowlands (300 m, black solid curve) and highlands (3250 m, green dashed curve) is calculated within concentric spherical shells. Most species are densely clustered towards the centre of morphospace, particularly in the lowlands.

with expectations under the null model (figure 2), potentially implying that both components contribute more or less equally to changes in richness. However, when we quantified niche packing between assemblages, we found that the majority of the additional species at lower elevations occur within the range of trait space occupied at higher elevations (figure 3a). The percentage of richness attributable to this kind of packing was 93% when lowlands were compared with mid-elevations (1600 m) and 78% when they were compared with high elevations (3250 m) (figure 3b). This dominant trend of niche packing was driven by insectivores, whereas niche expansion and packing had more equal contributions when calculated for other feeding groups, again depending on whether the comparison was made with mid-elevation (58– 74%) or highland (36%) assemblages (figure 3b). Finally, our results show that this strong tendency towards niche packing arises despite large increases in morphovolume (figure 2), because within assemblages most species are concentrated in a central core region of morphospace, with density declining rapidly towards the periphery (figure 3c).

(c) Ecological specialization

Dietary specialization was independent of species mid-point elevation (slope = −0.01, $p = 0.96$). In contrast, species attack manoeuvres were significantly more specialized at high elevations (slope = 0.49, $p < 0.05$) while specialization in substrate use declined towards the highlands (slope = −0.59, $p < 0.05$). When accounting for species phylogenetic non-independence, we found no relationship between elevation and specialization in diet, foraging manoeuvre or substrate (electronic supplementary material, table S7).

4. Discussion

The idea that the greater richness of tropical or lowland assemblages is associated with an expansion in the volume of available niche space provides one of the most compelling explanations for latitudinal and elevational gradients in diversity [4,6]. The volume of niche space may increase in the tropics through multiple mechanisms, including greater energy availability and habitat complexity, as well as a relaxation of the biophysical limitations imposed by cold or highly seasonal environments [22]. These effects may cascade across trophic levels. For instance, Schoener [11] showed that tropical insectivorous birds spanned a much wider range of beak sizes than temperate zone insectivores, attributing this to the greater diversity of available prey sizes. Our study extends this finding across different ecological guilds and traits by showing that elevational gradients in passerine richness are associated with an expansion in the volume of functional trait space towards the tropical lowlands.

Although the increase in morphospace occupied at lower elevations provides some support for the niche expansion hypothesis, we found that assemblage morphovolume at any elevation was largely consistent with a null model in which traits are distributed at random across the gradient. Our results thus provide no evidence that species at the periphery of morphological trait space are selectively filtered out as richness decreases. This conclusion is consistent with our analysis of ecological guilds, the majority of which are represented across almost the entire elevation gradient, and only start to drop out at the highest elevations (greater than 3500 m), by which point richness is only a small fraction of lowland diversity. The greater volume of functional trait space in lowland assemblages thus appears to be primarily associated with an increasing number of 'variants on existing themes' rather than the occupation of major new regions of niche space.

In addition to the increase in morphovolume, we found that trait distances between co-occurring species declined continuously towards the lowlands, supporting the idea that increases in richness are strongly associated with denser niche packing. The increase in morphodensity, as with volume, was no greater than expected under the null model, perhaps implying that trait packing and expansion contribute equally to the gradient in richness. However, across all elevations, most species were concentrated within a central core region of trait space, with the density of species declining rapidly towards the periphery [37]. Thus, increases in trait volume were driven by a relatively small number of species with extreme phenotypes, while most (78%) of the additional diversity in the lowlands was accommodated within a volume of functional trait space equivalent to that occupied in the highlands. When measured in this way, the trend towards greater trait packing far exceeds that of increasing trait volume across the gradient of species richness.

The relationship between increased morphodensity and species richness towards the lowlands was consistent across most guilds and families, but in some cases these trends were decoupled. For instance, in tyrant-flycatchers (Tyrannidae), distances between nearest neighbours in trait space remained relatively constant from 3000 m to the lowlands despite a continuous increase in richness. This pattern implies that there may be constraints on the similarity of coexisting tyrant-flycatcher species, but that such limits do not constrain assemblage richness, at least in the context of this particular clade and its contribution to the world's richest elevational transect. More generally, limits to phenotypic similarity predict that the evenness of trait spacing may increase at higher species richness [40]. However, our results reject a simple monotonic trend of increasing functional evenness with richness and instead show that the evenness of trait packing first declines from high to mid-elevations before then increasing towards the lowlands. While the cause of this pattern remains unclear, our results provide no evidence that limits to phenotypic similarity constrain overall richness in the tropical lowlands.

One possible limitation of our approach is that morphological traits may be only weakly related to species ecological niches, in which case patterns of trait packing and expansion are likely to be uninformative. However, we are able to largely discount this possibility because we found that key dimensions of the ecological niche in passerines, including diet, foraging manoeuvre and foraging substrate were, to varying extents, predictable on the basis of phenotypic traits. Furthermore, we

found that while predictability increased with the number of traits sampled, the addition of each subsequent trait contributed a diminishing improvement to model fit. These results suggest that the traits we measured are sufficiently informative to capture major dimensions of the ecological niche and, together with previous findings [25], provide strong support for the use of species traits in quantifying changes in the partitioning of niche space within avian assemblages.

This still leaves open the possibility that major niche axes are not adequately captured by functional traits, perhaps exaggerating the trend towards greater niche packing in the lowlands. For example, the higher number of habitat strata in lowland tropical forest may allow vertical segregation of ecological competitors with similar traits, facilitating coexistence without direct contact [6,27]. However, because ecological adaptations to different vegetation strata are also associated with consistent biometric differences in traits such as tarsus or wing length [25,42], we expect that these effects should also be detected in our analyses.

While we found that different guilds map onto different regions of morphospace, these guilds could not be completely discriminated on the basis of their traits. Thus, species that are close neighbours in trait space may in some instances occupy rather distinct niches, and our analysis of morphological traits may thus overestimate the extent of niche packing. Indeed, when we repeated our analyses within individual guilds, we found that the strength of trait packing across the gradient was reduced. An alternative explanation for this finding, however, is that basic ecological guilds do not actually represent completely distinct regions of niche space and that phenotypic traits capture the similarity in species niches more accurately than guild classifications. For example, the overlap in morphospace of omnivores and specialist insectivores seems likely to reflect real similarities in diet, foraging behaviour and substrate. These findings raise important questions about how phenotypic and ecological traits should be combined when testing patterns of niche structure, but on the basis of our results, we suspect that the levels of niche packing detected within guilds are likely to be highly conservative.

Overall, our results suggest that while the precise contribution of niche packing will be difficult to resolve and is likely to depend on both context and methodology, gradients in passerine diversity are only weakly associated with an expansion in niche volume. Whether this pattern holds across all birds is open to question, but it seems likely given that passerines make up more than half of all avian diversity. Moreover, our results are consistent with earlier reports that average trait distances between species are smaller at low elevations for frugivores along the same gradient [23], and that the morphovolume of Himalayan songbird assemblages actually declines towards the lowlands [36]. Previous clade-level analyses across environmental gradients also reveal that the local richness of passerine families is largely unrelated to the volume of trait space they occupy [37]. Taken together, these findings suggest that increased niche packing, rather than niche expansion, is the dominant pattern underlying the high diversity of lowland tropical assemblages [6,43].

Although increased niche packing may arise through either narrower niche widths (i.e. finer specialization) or greater niche overlap [6], our analysis of mean species trait values is unable to separate these possibilities. It is often proposed that tropical lineages are more highly specialized than temperate zone lineages [4,10], and it has been suggested,

based on niche width estimates in insects [44], that finer niche specialization may also underlie elevational diversity gradients. However, evidence for gradients in niche specialization in birds derives mainly from anecdotal case studies [45] or global analyses necessarily limited to using relatively coarse indices of niche width (e.g. major diet and habitat classifications) [13], whereas more detailed tests have provided inconsistent support for this hypothesis (e.g. [16,18]). Here, we found no evidence for an increase in specialization towards the lowlands at the scale of either diet or foraging manoeuvre and while the variety of substrates used by gleaning and sallying insectivores increased with elevation, this pattern disappeared when accounting for species phylogenetic relatedness. Thus, rather than representing a general trend, we cannot rule out the possibility that differences in niche width simply reflect the presence of one or a few highly specialized clades in the lowlands. The role of greater niche specialization in accommodating the denser trait packing in the tropical lowlands therefore remains unresolved.

The link between high diversity and packed niches has been a longstanding conundrum in ecology, enshrined in Hutchinson's 'paradox of the plankton' [46] and inspiring Hubbell's neutral theory [9], but few studies have attempted to explore this pattern in vertebrate assemblages across entire geographical gradients using functional traits explicitly linked to the dietary niche. The two alternative models of niche occupancy considered here—niche expansion and niche packing—were originally developed assuming equilibrium levels of diversity, but they may also reflect historical processes, including differences in the rates or time available for niche evolution, speciation, dispersal and extinction. Although it is not possible to disentangle the underlying causes, our results provide strong support for the niche packing model as the predominant trend underlying gradients in avian species richness. An understanding of the extent to which greater niche packing reflects niche overlap or specialization will require more detailed information on relevant niche axes, such as microhabitat use, foraging behaviour and diet, across broad-scale environmental gradients.

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