



# Dynamic trait-niche relationships shape niche partitioning across habitat transformation gradients

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## Abstract

Multidimensional approaches examining complex trait-niche relationships are crucial to understand community assembly. This is particularly important across habitat transformation gradients because specialists are progressively substituted by generalists and, despite increasing functional homogenization, in both specialist and generalist communities niche partitioning is apparent. Here, in line with the continuum hypothesis, we expected that divergent trait-niche relationships would arise in passerine assemblages across the natural-to-urban transformation gradient. More specifically, we expected that traits linking form to function would be more important in less transformed habitats, while population density and traits linked to dispersal and dominance would predominate in more transformed habitats. Accordingly, we found that beak length and its interaction with tarsus length correlated significantly with isotopic niches in natural and rural habitats, where specialists predominate. Conversely, body size and aggressiveness only showed significant relationships with isotopic niches with increasing habitat transformation, where generalists prevail. Interestingly, we recorded a mix of these processes in rural habitats, which acted as a frontier between these two domains. Our study is thus important in showing that a complex combination of morphological and behavioral traits determine niche characteristics, and that these relationships are dynamic across habitat transformation gradients.

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## Introduction

Over millions of years, animal species have evolved morphological and behavioral adaptations enabling highly efficient exploitation of certain habitats and food resources,

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which facilitate species coexistence through competition avoidance (Tokeshi, 2009). For example, hummingbirds have refined beak morphologies matching the shape of the flowers from which they extract nectar (Jordano, 1987). Herbivore mammals inhabiting the African savannah have body morphologies adapted to exploit different strata of the available plant resources (Kleynhans et al., 2011). African Cichlid fishes evolved complex mouth morphologies finely adapted to specialized foraging strategies (Albertson et al., 2005). Therefore, there is often a fine match between specialists' functional traits, i.e. traits linking form to function, and their niches – an n-dimensional space where a species can exist (Hutchinson, 1957). These relationships are commonly referred to as trait-niche relationships. However, our planet has periodically experienced profound and abrupt environmental changes, so that becoming excessively specialized may make species less resilient to environmental perturbations (Alvarez et al., 2019).

Across the last centuries, and accelerating in the last decades, a human-driven sudden change is altering Earth's environmental conditions, which is commonly referred to as the Anthropocene (Lewis & Maslin, 2015). This process is producing strong disturbances in the normal functioning of Earth's ecosystems, erasing million-year-old species interactions, and inducing the collapse of complex trophic webs (Emer et al., 2019; Pringle et al., 2019). More specifically, environmental changes modifying habitat structure and the availability of resources are strongly detrimental for specialists, so that this group is progressively substituted by generalists across habitat transformation gradients (Ducatez et al., 2018). Species turnover often results in a simplification of these communities, meaning that species in communities in transformed habitats often are less specialized than species in natural communities, a process commonly labelled functional homogenization (Devictor et al., 2008). Understanding how biodiversity loss associated with environmental change disrupts ecosystem functioning is thus fundamental before millions of years of evolutionary history are irreversibly lost (Sol et al., 2017).

Interestingly, functional homogenization does not necessarily imply that species' realized niches are redundant, i.e., that there is increased niche overlap. Communities of specialists and generalists may show comparable levels of niche partitioning facilitating species' coexistence (Liang et al., 2020; Pagani-Núñez et al., 2019). To overcome this paradox, and in line with the "continuum hypothesis" (Gravel et al., 2006), species would need different sets of traits and dynamic trait-niche relationships to maintain differentiated niches across transformation gradients. Trait-niche relationships linking form to function, i.e. morphological traits directly related to niche use (Pigot et al., 2020), would be relevant where specialists' links to their resources may be unaltered. In contrast, with increasing habitat transformation and functional homogenization, other traits would drive niche partitioning. For instance, population density effects would confer a central, dominant, niche position to

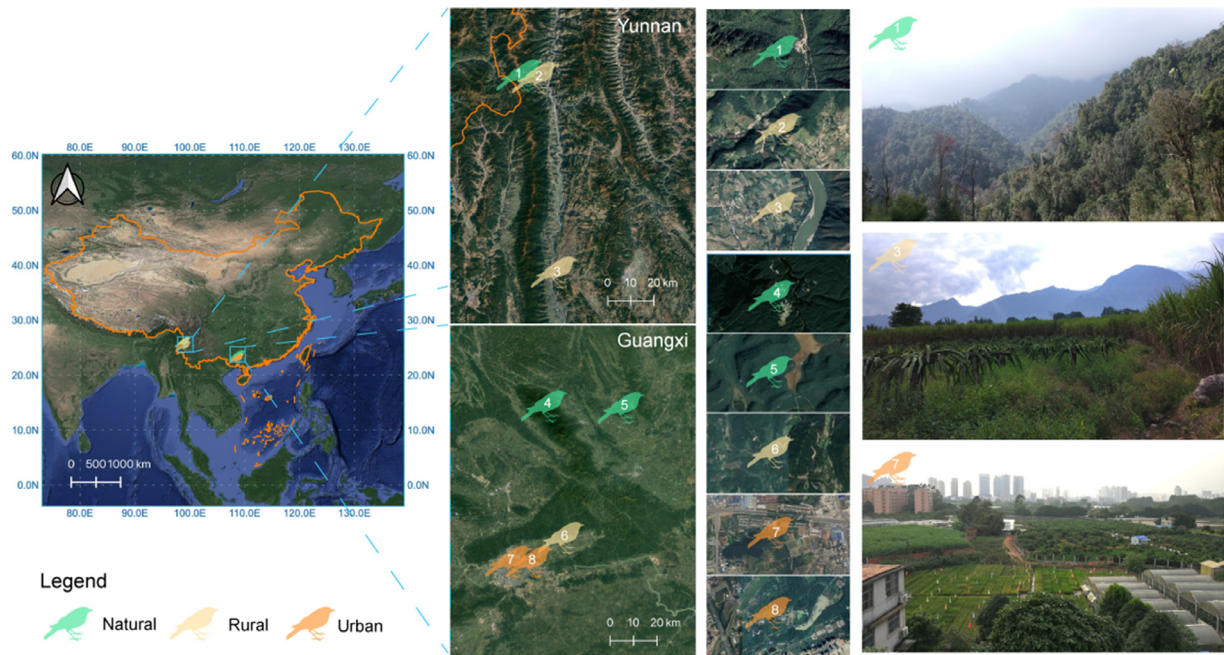
more abundant species (Thompson et al., 2020; Vela Díaz et al., 2020). Similarly, dispersal capacity would facilitate species' niche expansion (Bastianelli et al., 2017; Salisbury et al., 2012). Finally, body size and aggressiveness would enable species to maintain differentiated niches (Martin & Bonier, 2018; Ulrich et al., 2018).

Here, we assessed trait-niche relationships across natural-to-urban transformation gradients in eight highly diverse, subtropical passerine assemblages. Birds are highly suitable to study this question due to their high taxonomic and functional diversity and broad variety of responses to environmental change (Bregman et al., 2014; Sol et al., 2020). To do this, we used  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotopes to quantify species' realized niches, namely niche width and overlap (Pagani-Núñez et al., 2019). Stable isotopes provide continuous metrics of resource use and integrate both habitat use ( $\delta^{13}\text{C}$ ) and trophic level ( $\delta^{15}\text{N}$ ) (Boecklen et al., 2011; Pagani-Núñez, Renom, et al., 2017). We also took comprehensive behavioral and morphological measurements. In doing so, we overcome implicit limitations imposed when relying on diet categories or single-trait approaches (Pigot et al., 2020). We formulated several predictions. We expected a contraction of the morphological trait space, namely functional homogenization, across the habitat transformation gradient (Callaghan et al., 2019). Moreover, we expected that divergent trait-niche relationships would arise across these gradients. In natural habitats, we expected that specialized morphologies (particularly long beaks and the ratio between different body traits) would be the main drivers of niche partitioning, i.e., these traits would show a negative relationship with niche overlap. For instance, the ratio between beak and tarsus length is indicative of specialization to forage on the ground or the canopy, and that between tarsus and wing length is indicative of specialization to capture insects in flight or using short leaps (Remsen & Robinson, 1990). Conversely, in transformed habitats, we expected that high population densities, larger body sizes and high dispersal capacity would be linked to larger niche width, while high aggressiveness would be linked to reduced niche overlap. This study contributes to expanding our knowledge about how environmental change affects ecosystem functioning by ascertaining how habitat transformation modifies trait-niche relationships in highly diverse animal communities.

## Materials and methods

### Study area and field procedures

We collected data from eight passerine assemblages during 2016 and 2017 using 70 m of mist nets at fixed sites in a broad area across Yunnan Province (Southwest China) and Guangxi Zhuang Autonomous Region (South China) (Fig. 1). This is a subtropical region according to the Köppen climate classification (Zheng, 2000), harboring rich biodiversity yet also experiencing intense habitat transformation (Dai et al., 2018; Pan et al., 2019). We categorized



**Fig. 1.** Map of our study areas. From left to right, geographical map of the People's Republic of China highlighting our study areas, depiction of our two study regions: Yunnan Province and Guangxi Zhuang Autonomous Region, depiction of our eight study locations, and three pictures illustrating habitat differences across the transformation gradient. Pictures of study sites taken by the authors.

them into natural (3 sites), rural (3 sites), or urban (2 sites) (Fig. 1). Natural sites were primary or secondary forests with little human activity. Rural sites were areas where agriculture and silviculture predominated. Urban sites were urban parks. We captured a total of 1068 individuals from 137 species. Species diversity was generally high, with rarefied richness ranging from 13.90 (natural site) to 31.00 (rural site). Average rarefied richness was 20.26 for natural sites, 26.69 for rural sites, and 22.58 for urban sites. Thus, all the sites harbored relatively high diversity (Mann-Whitney U Tests of differences in rarefied richness between pairs of habitat types all had  $P$ -values  $> 0.40$ ). Sampling duration and elevation had negligible effects on niche characteristics and were not included in our analyses (Pagani-Núñez et al., 2019).

We captured birds in suitable places with abundant vegetation cover. In five sites in Guangxi (2 urban, 1 rural and 2 natural), we followed a constant effort protocol by visiting each location at least once per month, except during July and August 2016 when temperatures were extremely high ( $> 40^{\circ}\text{C}$ ). In these sites, we left the nets open for six hours after dawn during two consecutive days in each visit. In three remote sites in Yunnan (2 rural and 1 natural), we followed an intensive approach, working during several consecutive days and leaving the nets from dawn to dusk. We checked mist nets every hour, and every 30 minutes when temperature exceeded  $30^{\circ}\text{C}$ . We banded individual birds with numbered plastic rings and released them near the places at which they were captured, once morphological and behavioral measurements were taken. We excluded recaptured individuals from our analyses.

## Behavioral and morphological measurements

We carefully extracted the captured birds and put them into separate cloth bags for at least 5 minutes before taking any measurements. We measured behavioral traits first because handling may result in considerable behavioral changes (Senar et al., 2017). To characterize aggressiveness, we measured breath and pecking rates, and the number of distress calls (Koolhaas et al., 1999). These traits are optimal proxies of proactivity and aggressiveness (Carere & van Oers, 2004). We first took breath rate, holding the bird over our open hand and counting the number of breaths for 30s (Liang et al., 2018; Senar et al., 2017). We then quantified pecking rate as the number of pecks or bites to the handler, holding a finger vertically in front of the bird for 15 s (Senar et al., 2017), and recording the number of distress calls emitted during the same period. Most species in our sample showed no or little sexual dimorphism, and little differences in breath rate (Liang et al., 2018), so we assumed negligible sex effects on behavioral traits.

Then, we recorded body mass to the nearest 0.1 g using an electronic balance, and wing (of both primary and secondary feathers), tail, tarsus and beak length to the nearest mm using a digital ruler. We computed the Hand-Wing-Index (HWI), as the Kipp's distance corrected for wing size (i.e., the difference between primary and secondary length), commonly used as a proxy of dispersal capacity (Paradis et al., 1998; Sheard et al., 2020). We also computed population density as the number of individuals captured per meter of net and hour ( $\text{N}/\text{m}^*\text{h}$ ). We required at least 5 individuals per species in each population to compute niche characteristics

(see below), so we only used data from such species. We computed the average values for each trait using the individuals of a given species in each site (for each population). The first author collected field data and trained together with Dan Liang and Chao He for months to guarantee that in some instances in which the first author could not be in the field the collected data was comparable.

## Quantifying niche characteristics

For stable isotopic analyses, we cut the tip of the claws as the isotopic ratio of tip claws represents the diet information over weeks to months depending on the size of the claw (Bearhop et al., 2003). We measured carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) stable isotopes of claws from all individuals in each community. Samples were cleaned with a NaOH (0.25 M) solution, air-dried for at least 12 hours, and weighed (0.35 mg) into tin capsules. The abundances of  $^{13}\text{C}/^{12}\text{C}$ ,  $^{15}\text{N}/^{14}\text{N}$  were determined at the Guangxi University Stable Isotopic Laboratory using an elemental analyzer with an isotope ratio mass spectrometer via a continuous flow interface. Stable isotope ratios were converted using the equation:  $\delta X (\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$ , where X is  $^{13}\text{C}$  or  $^{15}\text{N}$  and R is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ , and then referenced against the international standards: Pee Dee belemnite for  $^{13}\text{C}$ , and atmospheric nitrogen for  $^{15}\text{N}$ . The precisions of measurements were 0.15% for  $\delta^{13}\text{C}$  and 0.25% for  $\delta^{15}\text{N}$ , respectively.

We quantified niche width and overlap of species with at least five individuals in at least one assemblage (Pagani-Núñez et al., 2019). This procedure reduced our dataset to 608 individuals of 29 species, of which nine species were present in at least two assemblages (2 to 4 assemblages), yielding a total of 42 populations in our dataset. We computed niche width as the standard ellipse areas corrected by sample size (SEAc) of the isotopic space of each population using SIBER v2.1.4 (Jackson et al., 2011). SEAc are geometric representations of a population's niche space, so that populations with individuals showing higher variability in stable isotopes would produce a larger ellipse area and vice versa. We computed niche overlap as the average overlap of a species with all the other species in each assemblage (i.e., of each population in each assemblage). Niche overlap was quantified using nicheR-over v 1.0, which relies on a Bayesian resampling approach understood as the probability of an individual of a given species/population to be recorded in the niche space of a second species/population (Swanson et al., 2015).

## Statistical analyses

We performed all analyses in R v3.6.1 (R Core Team, 2021). Morphological and behavioral traits are likely correlated with each other and co-vary across axes such as body size (Pigot et al., 2020). Hence, we computed two

principal component analysis (PCA) with scale transformation, one for morphological traits (body mass and wing, tail, tarsus, and beak length) and another for behavioral traits (pecking and breath rate, and number of distress calls), summarizing their relationships. We decided not to control for phylogenetic relatedness at this stage because we did so in all further analyses. We only considered variable scores over 0.50 and component eigenvalues higher than 1. We set the number of dimensions to reach 100% of explained variance. We obtained two main components from the PCA on morphological traits (“body size”) and one from the PCA on behavioral traits (“aggressiveness”) fulfilling these criteria and aligned with our predictions, which were used as predictors in our models (Supplementary Material S1). We also obtained a potentially interesting component from the PCA on morphological traits (beak vs tarsus length, which we labelled “body morphology”), yet with an eigenvalue slightly lower than 1 (Supplementary Material S1). For instance, species with long tarsi and short beaks would be particularly well adapted to forage on a broad diversity of prey on the ground, while species with short tarsi and long beaks would be adapted to exploit prey found within trees’ bark (Remsen & Robinson, 1990). Therefore, we included this component in our analyses but also ran models using beak and tarsus length. In summary, we considered six variables characterizing species morphology and behavior (body size, body morphology, aggressiveness, beak and tarsus length, and the HWI), and population density.

All further analyses accounted for species’ phylogenetic relatedness. We computed a phylogenetic tree by downloading 10000 Markov chain Monte Carlo (MCMC) backbone phylogenies of the 29 target species and generated the Maximum Clade Credibility (MCC) tree using the function “max-CladeCred” in the package phangorn v2.5.5 (Schliep, 2011). To include all populations of nine species with more than one population, we modified the MCC tree by manually adding small branches ( $10^{-10}$ ) between conspecific populations (Pagani-Núñez et al., 2019).

Firstly, we determined whether there were differences in morphological and behavioral traits across habitat types to understand how habitat transformation shaped the trait space. To do this, we constructed Phylogenetic Generalized Least Squares (PGLS) models for each dependent variable (body size, body morphology, aggressiveness, beak length, tarsus length, and the HWI) using the package caper v1.0.1 (Omer, 2018). We included habitat type (natural, rural, or urban) as categorical factor. We computed the phylogenetic signal lambda ( $\lambda$ ) for each model. The body size model did not converge, so that we used instead a phylogenetically controlled Markov chain Monte Carlo generalized linear mixed model (MCMCglmm) for that variable using the package MCMCglmm v2.30 (Hadfield, 2010). We set the model to run 75000 iterations, with a thinning interval of 40 and a burn-in of 7500.

Secondly, we determined which traits were more important in explaining variability in niche characteristics. We

constructed two PGLS models including niche width and overlap as dependent variables and body size, body morphology, aggressiveness, HWI, and population density, as predictors. We ran two additional models using beak and tarsus length, instead of the component body morphology. We improved model performance by applying a model selection and averaging approach using the package MuMIn v1.43.17 (Burnham & Anderson, 2002). We ranked the subset models based on their Akaike's Information Criterion corrected for small sample sizes (AICc) and averaged the coefficients of the selected models ( $\Delta\text{AICc} < 2$ ) (Burnham & Anderson, 2002).

Finally, we tested our prediction that divergent trait-niche relationships would arise across the habitat transformation gradient using a PGLS approach. Our dependent variables were niche width and overlap. We ran a model for the variables selected in the previous section: population density, the HWI and aggressiveness for niche width, and body size, body morphology, aggressiveness, beak length, tarsus length and the HWI for niche overlap. In each model, we analyzed the interaction between each of these predictors and habitat type (natural, rural, or urban). We constructed thus a total number of 9 models.

The absolute values of correlation coefficients ( $|r|$ ) between the continuous predictors (the three components, beak and tarsus length, the HWI and population density) were less than 0.7, suggesting no significant collinearity between them (Dormann et al., 2013). As habitat type had three levels (natural, rural, and urban), we dummy-coded these levels and repeated the analyses using a different level as a reference to perform comparisons between each pair of habitat types. All continuous variables, except for the PCA components, were scaled (mean of 0 and SD of 1) in all analyses to improve homoscedasticity and model performance.

## Results

### Differences in morphological and behavioral traits across habitat types

The morphological trait space became narrower across the transformation gradient (Fig. 2A). Accordingly, the component body morphology showed higher values in natural than in urban habitats (Natural vs Urban:  $\beta \pm SE = -0.78 \pm 0.30$ ,  $z = -2.63$ ,  $P = 0.01$ ) (Supplementary Material S2; Fig. 2B), meaning that birds in natural habitats had on average longer beaks and shorter tarsi than those in urban habitats. There were no other significant differences between habitat types in body morphology. We also examined directly differences in beak and tarsus length between habitat types. We found that populations in natural habitats had longer beaks than in rural habitats (Natural vs Rural:  $\beta \pm SE = -3.97 \pm 1.85$ ,  $z = -2.14$ ,  $P = 0.04$ ) (Supplementary Material S2; Fig. 2C),

while urban populations showed no differences with populations in rural and natural habitats. We recorded no significant differences in tarsus length, body size, HWI or aggressiveness (Fig. 2D) between habitat types (Supplementary Material S3).

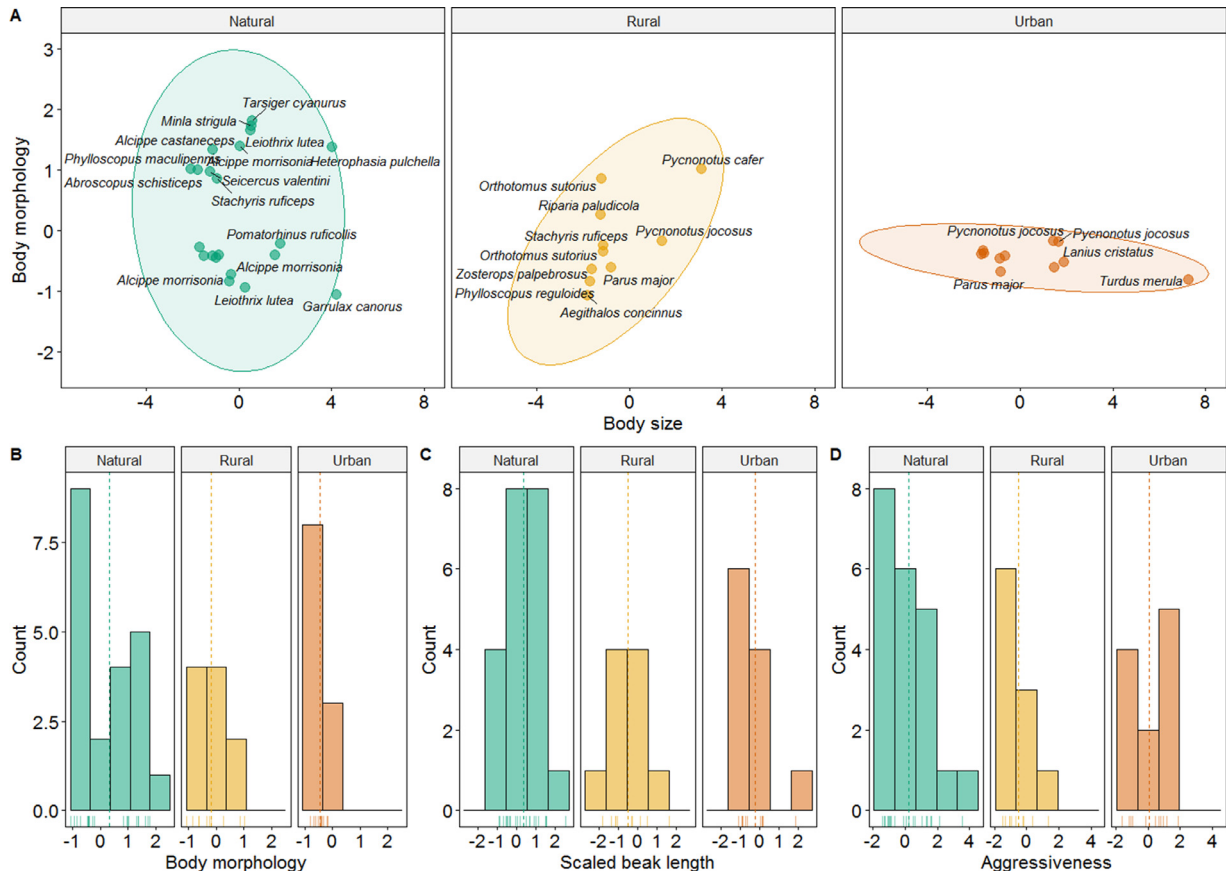
### Relative importance of niche and neutral traits for niche characteristics

None of the morphological and behavioral traits, nor population density, showed significant effects on niche width when pooled together in a single model, either using the component body morphology, or beak and tarsus length directly (Supplementary Material S4). However, the component body morphology correlated negatively with niche overlap (Table 1A), meaning that birds with longer beaks and shorter tarsi had lower overlap. Other morphological and behavioral traits, and population density, showed no effects on niche overlap. The model using beak and tarsus length instead of the component body morphology depicted slightly different results. Beak length and the HWI correlated negatively with niche overlap (Table 1B), meaning that birds with longer beaks and more pointed wings had lower overlap. The other variables showed no significant effects on niche overlap.

### Habitat transformation effects on trait-niche relationships

The HWI and population density showed no significant relationships with niche width within any of the habitat types (Supplementary Material S5). The component aggressiveness showed a negative relationship with niche width in urban habitats (Table 2A; Fig. 3A), meaning that birds displaying more aggressive behaviors (higher pecking rates, more distress calls, and lower breath rate) had narrower niches, while this relationship was not significant in rural or natural habitats.

We recorded significant negative relationships between niche overlap and the component body morphology in both natural and rural habitats, yet not in urban habitats (Table 2B; Fig. 3B). Beak length also showed significant negative relationships with niche overlap in both natural and rural habitats, meaning that birds with longer beaks had lower overlap, yet not in urban habitats (Table 2B; Fig. 3C). Tarsus length showed no significant relationships with niche overlap within any of the habitat types (Supplementary Material S5). The component body size showed no significant relationships with niche overlap in any habitat type, yet the negative relationship in rural habitats showed high effect size and a marginally significant P-value (0.05) (Table 2B). The component aggressiveness and the HWI showed no



**Fig. 2.** (A) Relationships between the principal component analysis components body morphology (beak vs tarsus length) and body size for 44 populations of 29 passerine species in 8 locations across habitat transformation gradients (natural, rural, or urban). Ellipses show 95% normal-probability areas superimposed over the data points. Species’ Latin names are depicted besides each data point. Additionally, histograms showing data distribution across habitat types (natural, rural, or urban) for (B) the principal component analysis component body morphology (beak vs tarsus length), (C) scaled beak length, and (D) the principal component analysis component aggressiveness (pecking rates and distress calls vs breath rate). Vertical dashed lines represent mean values.

**Table 1.** **A)** Results of the phylogenetic generalized least squares regression (PGLS) using niche overlap as dependent variable, and the principal component analysis components body size, body morphology (beak vs tarsus length), aggressiveness (pecking rates and distress calls vs breath rate), the Hand-Wing Index (HWI), and population density (N/m/h) as continuous predictors. **B)** We ran an additional model directly using beak and tarsus length (mm) instead of the component body morphology. We used model selection and averaging based on Akaike Information Criteria scores ( $\Delta AICc < 2$ ) and computed conditional averages (only selected models). Number of models in which a variable was included and its importance (sum of model weights over models including the variable) is provided. All the variables, except for PCA components, were scaled to improve homoscedasticity and model performance. Significant effects are marked with bold.

	$\beta$	SE	z	P	N models	Importance
<b>A</b>						
Intercept	< 0.01	0.13	< 0.01	1.00		
Aggressiveness	-0.19	0.12	1.6	0.11	3	0.52
<b>Body morphology</b>	<b>-0.67</b>	<b>0.15</b>	<b>4.49</b>	<b>&lt; 0.01</b>	<b>6</b>	<b>1.00</b>
Body size	-0.14	0.1	1.39	0.17	3	0.42
HWI	-0.28	0.2	1.42	0.16	3	0.42
<b>B</b>						
Intercept	< 0.01	0.12	< 0.01	1.00		
<b>Beak length</b>	<b>-0.72</b>	<b>0.15</b>	<b>4.87</b>	<b>&lt; 0.01</b>	<b>3</b>	<b>1.00</b>
<b>HWI</b>	<b>-0.46</b>	<b>0.17</b>	<b>2.68</b>	<b>0.01</b>	<b>3</b>	<b>1.00</b>
Aggressiveness	-0.14	0.12	1.1	0.27	1	0.29
Tarsus length	0.13	0.18	0.72	0.47	1	0.20

**Table 2.** A) Results of phylogenetic generalized least squares regression (PGLS) using niche width as dependent variable, and the interaction between habitat type (natural, rural, or urban) and the PCA component aggressiveness (pecking rates and distress calls vs breath rate) as continuous predictors. B) We ran additional models using niche overlap as dependent variable, and the interaction between habitat type (natural, rural, or urban) and body morphology, beak length (mm) and the PCA component body size as continuous predictors. All the variables (except for PCA components) were scaled to improve homoscedasticity and model performance. Significant effects are marked with bold.

	$\beta$	SE	z	P
<b>A - Niche width</b>				
$(\lambda = 0.86, R^2 = 0.06)$				
Intercept	0.94	0.46	2.04	0.05
Aggressiveness*natural	0.10	0.13	0.73	0.47
Aggressiveness*rural	-0.32	0.26	-1.20	0.24
<b>Aggressiveness*urban</b>	<b>-0.50</b>	<b>0.23</b>	<b>-2.20</b>	<b>0.03</b>
<b>B - Niche overlap</b>				
$(\lambda = 0.00, R^2 = 0.33)$				
Intercept	-0.10	0.15	-0.64	0.53
<b>Body morphology*natural</b>	<b>-0.53</b>	<b>0.18</b>	<b>-2.97</b>	<b>0.01</b>
<b>Body morphology*rural</b>	<b>-1.17</b>	<b>0.38</b>	<b>-3.06</b>	<b>&lt; 0.01</b>
Body morphology*urban	-1.10	0.57	-1.92	0.06
$(\lambda = 0.00, R^2 = 0.23)$				
Intercept	0.04	0.15	0.29	0.77
<b>Beak length*natural</b>	<b>-0.62</b>	<b>0.20</b>	<b>-3.12</b>	<b>&lt; 0.01</b>
<b>Beak length*rural</b>	<b>-0.56</b>	<b>0.26</b>	<b>-2.13</b>	<b>0.04</b>
Beak length*urban	-0.05	0.31	-0.15	0.88
$(\lambda = 0.00, R^2 = 0.05)$				
Intercept	-0.07	0.15	-0.44	0.66
Body size*natural	-0.10	0.13	-0.80	0.43
Body size*rural	-0.39	0.19	-2.05	0.05
Body size*urban	0.06	0.12	0.55	0.59

significant relationships with niche overlap in any habitat type (Supplementary Material S5).

## Discussion

Multidimensional trait approaches examining dynamic interactions between functional traits and multiple dimensions of niche use, and considering species' evolution, are fundamental to ascertain community assembly rules and niche structure dynamics (Cadotte et al., 2013; Kraft et al., 2008). In this study, we found support to our hypothesis that specialized morphologies directly linked to resource use (beak length and the ratio between beak and tarsus length) would decrease in importance in predicting niche characteristics with increasing habitat transformation (Fig. 3). Other traits such as aggressiveness and body size determined niche width and overlap in transformed habitats, suggesting a profound change in how these communities are structured. This

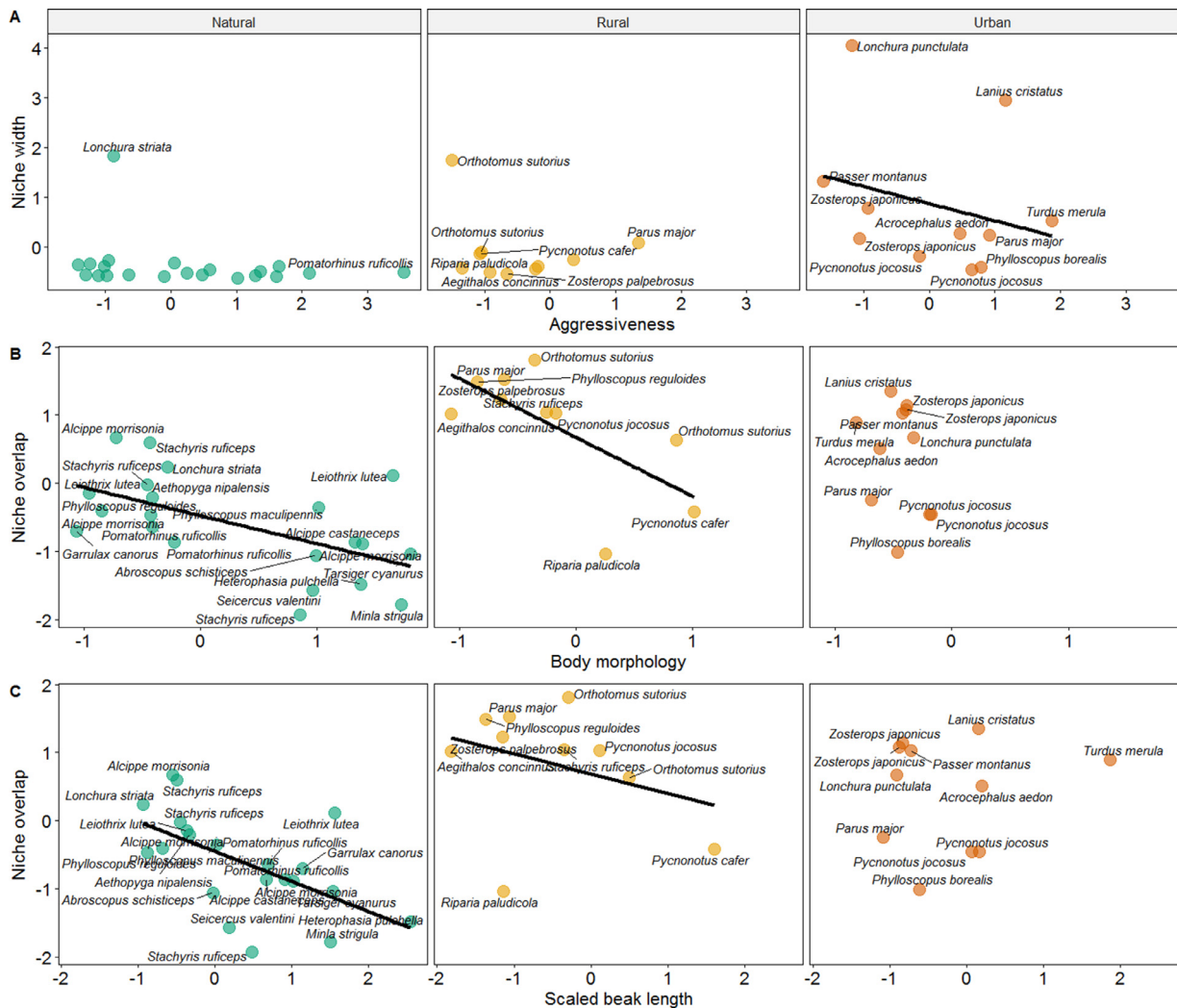
change was probably elicited by a contraction of the morphological trait space and species' need to exploit broader niches to guarantee population viability, across this gradient. Nevertheless, some of these results were unexpected. Aggressiveness was linked to smaller niche widths rather than to lower niche overlap in urban habitats, and larger body sizes were linked to lower niche overlap rather than larger niche widths in rural habitats. All in all, these findings are important in suggesting that a combination of morphological and behavioral traits – rather than single traits (Pigot et al., 2020) – determine niche characteristics, and that these relationships are dynamic across habitat transformation gradients (Gravel et al., 2006).

## Trait-niche relationships and niche partitioning in transformed habitats

Morphology and behavior determine species' function and position in communities and ecosystems (Ferry-Graham et al., 2002). Across the last decades, many studies have regarded specialized morphologies as the main driver of niche partitioning in assemblages of closely related species. For instance, bats and fishes partition their niches according to highly evolved morphologies and refined foraging techniques that enable the exploitation of particular prey types (Aguirre et al., 2002). Similarly, birds are relatively specialized animals and strict omnivory is rather uncommon (Burin et al., 2016). Surprisingly, previous studies have shown a relatively weak match between form and function – i.e. between morphological traits and niche position – in birds (Pigot et al., 2020; Ricklefs, 2012), inverse relationships between microhabitat use and morphological specialization in tropical fishes (Brandl et al., 2015), and divergent mechanisms allowing coexistence between old and young avian lineages (Laiolo et al., 2017). We found that morphological traits determined niche overlap in natural and rural habitats, while increased aggressiveness was only linked to narrower niche widths in urban habitats. Therefore, our results illustrate highly dynamic trait-niche relationships by exploring the association among its multiple dimensions and in the context of habitat transformation. Our study is thus in line with a growing body of literature suggesting that a combination of niche and neutral processes drive community structure and assembly rules (Burson et al., 2019; Simmons et al., 2020).

## Biotic homogenization and species' complementarity

Generalist species can be considered functionally equivalent and thus are often regarded as redundant, a pattern particularly evident in transformed habitats (Devictor et al., 2008; McKinney, 2006). However, functionally similar



**Fig. 3.** Relationships between trait and niches characteristics for 44 populations of 29 passerine species in 8 locations across habitat transformation gradients (natural, rural, or urban). (A) Relationship between principal component analysis component aggressiveness (pecking rates and distress calls vs breath rate) and niche width (Standard Ellipse Areas corrected by sample size) (aggressiveness vs niche width in urban:  $z = -2.20$ ,  $P = 0.03$ ), (B) relationship between the principal component analysis components body morphology (beak vs tarsus length) and niche overlap (body morphology vs niche overlap in natural:  $z = -2.97$ ,  $P = 0.01$ ; body morphology vs niche overlap in rural:  $z = -3.06$ ,  $P < 0.01$ ), and (C) relationship between scaled beak length and niche overlap (beak length vs niche overlap in natural:  $z = -3.12$ ,  $P < 0.01$ ; beak length vs niche overlap in rural:  $z = -2.13$ ,  $P = 0.04$ ). Regression lines are shown where these relationships were significant.

species likely have the need to partition available niches to a certain extent. Our findings support that niches are partitioned based on traits such as aggressiveness and body size in transformed habitats supports the view that this notion of redundancy can drive to misconceptions (Petchey et al., 2007). Interestingly, human disturbance and available human food resources have been linked to increased overlap in carnivore communities (Manlick & Pauli, 2020), yet previous studies have also suggested that alternative mechanisms, such as temporal and spatial segregation in response to human disturbance, could facilitate species coexistence (Di Bitetti et al., 2010; Schuette et al., 2013). In transformed habitats in our subtropical study system, food resources are relatively high. In addition to the comparatively small body size of birds and thus the capacity to sustain diverse

assemblages across small spatial scales (e.g., through vertical stratification) (Pagani-Núñez, He, et al., 2017), this would facilitate niche partitioning. Still, body size and aggressiveness shaped species' niches, suggesting that competitive interactions play a key role in structuring these assemblages.

## Conclusion

We recorded dynamic and heterogeneous trait-niche relationships across multiple dimensions of niche characteristics and axes of variation of morphological and behavioral traits. The relationships between traits and niches and the divergence in the traits explaining niche characteristics were



strong, so that they likely represent generalizable tendencies and might apply to other vertebrate taxa. Habitat transformation is a pervasive force eroding complex species interactions (Emer et al., 2019; Pringle et al., 2019). Consequently, species traits have variable importance in predicting niche characteristics in species' assemblages across the natural-to-urban gradient, hinting at complex responses to global change. Integrating individual to community level niche dynamics is fundamental to disentangle the inherent complexity of biodiversity patterns and community assembly rules in a rapidly changing world.

## Declaration of Competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:[10.1016/j.baae.2022.01.002](https://doi.org/10.1016/j.baae.2022.01.002).

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