Global patterns of specialization and coexistence in bird assemblages

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\textbf{ABSTRACT}

\textbf{Aim} Increased specialization has been hypothesized to facilitate local coexistence and thus high species richness, but empirical evaluations of the richness–specialization relationships have been relatively scant. Here, we provide a first assessment of this relationship for terrestrial bird assemblages at global extent and from fine to coarse grains.

\textbf{Location} World-wide.

\textbf{Methods} We use two indices of specialization that describe species-level resource use: diet and habitat specialization. The relationship between richness and mean assemblage-level specialization was independently assessed at realm, biome-realm, 12,100 km\textsuperscript{2} equal-area grid cells and fine-grained scales. To identify assemblages that are diverse relative to environmental conditions we: (1) applied quantile regressions, (2) statistically accounted for other environmental variables which may constrain richness, and (3) parsed the data according to the residuals of a model relating species richness to the environmental variables.

\textbf{Results} Assemblage species richness increases with both measures of specialization at all scales. Statistically, richness appears constrained by levels of specialization, with the highest richness values only found in specialized assemblages. Richness is positively associated with specialization even after accounting for gradients in resource availability. Net primary productivity and assemblage specialization have complementary statistical effects on assemblage species richness. Contrary to expectations based on niche partitioning of local resources, the relationship between specialization and richness is steep even at coarse scales.

\textbf{Main conclusions} The results demonstrate that for an entire clade, totalling > 9000 species, specialization and species richness are related, at least for diverse assemblages. The strong patterns observed across scales suggest that this relationship does not solely originate from (1) limits on coexistence in present-day assemblages, or (2) increased specialization in richer assemblages imposed by species’ abilities to partition ecological space. Instead, regional-scale influences on the species pool may determine much of the observed relationship between richness and specialization. Although causal attribution is not straightforward, these findings support the idea that, for the scale of our analysis, specialization may be related to the past origination of high-diversity assemblages, rather than their contemporary assembly.

\textbf{Keywords} Biodiversity, biological inventories, birds, diet breadth, habitat breadth, macroecology, regional scale, richness–specialization hypothesis, scale, species richness.
INTRODUCTION

Establishing a mechanistic and predictive understanding of global richness gradients is a central theme in community and macroecology. Generally, putative mechanisms have been approached from evolutionary or ecological perspectives. While evolutionary approaches focus on drivers of diversification, ecologists have emphasized the way assemblages subdivide niche-space locally and thus facilitate coexistence and high levels of species richness (Chase & Leibold, 2003). A prominent niche-based hypothesis for geographic variation in species richness asserts that certain environments, such as the tropics, support species that are more narrowly specialized and thus allow tighter species packing (Hutchinson, 1959; Connell & Orias, 1964; MacArthur, 1972).

A positive relationship between specialization and species richness has been put forward as a key explanation for global diversity gradients (MacArthur, 1972). Specifically, it has been argued that the latitudinal diversity gradient originates from the stable tropical climates, which allow narrower species tolerances and hence specialization (Klopfer & MacArthur, 1960; Pianka, 1966; MacArthur, 1972; Stevens, 1989; Jocque et al., 2010). However, while some researchers have found evidence for a positive relationship between specialization and species richness (sometimes using latitude as a proxy for richness; Pagel et al., 1991; Eeley & Foley, 1999; Cardillo, 2002; Dyer et al., 2007; Krashov et al., 2008b; Mason et al., 2008), others have not (Beaver, 1979; Lappalainen & Soininen, 2006; Novotny et al., 2006; Belmaker, 2009; Filippi-Codaccioni et al., 2010). Moreover, a meta-analysis failed to support the suggested richness–specialization association (Vázquez & Stevens, 2004).

Despite the prominence and potential relevance of the richness–specialization hypothesis, to date its empirical understanding has been limited. In this study we address this shortcoming by providing the first global assessment of specialization in relation to species richness for an entire large clade. We argue that a synthetic understanding of the purported effect of specialization on richness requires the additional consideration of two rarely examined issues: scale and context-dependence.

First, the strength and directionality of the richness–specialization relationship may change across scales. While some attention has been given to the scale-dependence of specialization within species (Krashov et al., 2008a; Devictor et al., 2010), few studies have explored the scaling of community-level specialization. If richness is limited by the ability to partition local resources, we may expect richness–specialization associations to be strong at fine scales, but weaker at regional scales where constraints on coexistence and effects of resource availability are unlikely to be major forces. If positive richness–specialization relationships were to arise under a scenario of richness driving specialization to facilitate the partitioning of resources (MacArthur, 1965; Rosenzweig & Ziv, 1999), we may similarly expect the patterns to be most pronounced at fine scales where resources are most limiting. Alternatively, richness–specialization associations at the assemblage level may primarily arise from regional-scale evolutionary diversification of lineages. For example, specialization may be associated with reduced dispersal and hence increased diversification rates (Jocque et al., 2010). As these evolutionary processes are manifested at a regional scale (Ricklefs, 2006), a positive richness–specialization relationship would accordingly be present at both regional and fine scales.

Second, the effect of specialization on species coexistence may depend on environmental conditions. When richness is depressed by external conditions (e.g. disturbance, dispersal limitation, harsh abiotic conditions), abiotic constraints are more likely than competition to structure species assemblages. We may therefore be more likely to observe a strong relationship between specialization and richness in assemblages that exist close to carrying capacity. Here we use estimates of net primary productivity and habitat heterogeneity to represent environmental constraints. Assemblages that contain more species than expected given environmental conditions are more likely to be limited by their ability to divide niche space. Thus, we expect to find context-dependence in the richness–specialization association: specialization may limit richness most strongly in assemblages that are species-rich relative to environmental conditions.

In this study we use birds to provide the first global exploration of the geography of specialization and its association with species richness, addressing both context- and scale-dependence. We expect richness–specialization relationships to be strongly positive, especially in assemblages that are species-rich relative to their environment, and steeper at fine than coarse scales. By assessing these relationships we expect to identify the role of specialization in global richness gradients.

MATERIALS AND METHODS

Assemblage data

Breeding season distributions for non-marine birds were compiled from the best available sources for a given region or taxonomic group (Jetz et al., 2007). Based on these distributions, species occurrence was determined within six realms (Afrotropics, Australasia, Indo-Malaya, Neartic, Neotropics and Palaearctic), 58 biome-realms (ecosystem type nested within realms; following Olson et al., 2001) and 9731 equal-area grid cells of 12,100 km² (110 × 110 km grids at the equator; cells with terrestrial surface < 20% or richness < 10 were excluded). Additionally, we compiled 398 fine-grained assemblages from an extensive survey of the literature for well-sampled and thoroughly documented species inventories (Meese, 2005; Belmaker & Jetz, 2011). Here we consider assemblages from areas of 10 to 7875 km² (median: 488 km², equivalent to 22 × 22 km grid cells) as fine-grained, with four larger assemblages in noticeably underrepresented regions (for an among-realm comparison see Fig. S1 in Appendix S1 in Supporting Information). Sub-setting the assemblages by area (30% largest vs. 30% smallest) gave qualitatively identical
results (Fig. S2 in Appendix S1). While these assemblages are fine-grained relative to typical macroecological studies, data limitations prevent us from extending these assemblages to yet finer grains, where biological interactions may increase in importance, without incurring geographic and environmental biases. Variation in fine-grained assemblage area was addressed by including area (log\(_{10}\)-transformed area in km\(^2\)) as a covariate in multi-predictor models. Following model diagnostics we log\(_{10}\)-transformed richness.

Specialization

We used two indices of specialization that describe species-level resource use: diet and habitat specialization. Diet specialization was estimated from a comprehensive literature survey, but based primarily on del Hoyo et al. (2008) (see Wilmán, 2011). Diet information included the proportional use (frequency of use relative to all other diet categories) of each of eight dietary categories (seeds, fleshy fruits, nectar, invertebrates, carrion, fish, other vertebrates, and other plant material). These were combined into a single value using the Levins’ index (Krebs, 1999):

\[
B = 1 - \frac{1}{\sum p_i^2}
\]

where \(p_i\) is the proportional use of dietary category \(i\).

Habitat specialization was estimated from the number of distinct habitats used by each species, as reported in a fine-scale IUCN assessment (Appendix S2). Critical to the analyses conducted here, the habitat specialization data are globally standardized. Although simplistic, counts of commonly used resources frequently perform as well as more detailed data (Krebs, 1999). Note that the number of distinct habitats returns values that are identical to those obtained from equation 1 when all used habitats are assigned equal proportions.

The maximum values of diet and habitat specialization indices will depend on the numbers of categories. We therefore standardized both dietary and habitat indices to vary between 0 and 1, and then subtracted this value from one so that higher index values indicate higher specialization:

\[
B_A = 1 - \frac{(B - 1)}{(n - 1)}
\]

where \(B\) is the unstandardized diet or habitat specialization index for each species and \(n\) is constant across all species and reflects the total number of dietary states (8) or the maximum number of habitats occupied by a species (12). Specialization indices displayed a left skew across species and assemblages, indicating that most species are specialized, and relatively few are generalists (Fig. 1). However, after performing a logit transformation (Warton & Hui, 2011) skew was substantially reduced (Fig. S3 in Appendix S1). We therefore used the mean across species of the logit-transformed specialization to represent assemblage-typical specialization values. Specialization values of one were given a value of 0.975 before transformation. Habitat and dietary specialization are considerably correlated (12,100 km\(^2\) grain: \(r = 0.68\)).

At least three unavoidable methodological limitations must be acknowledged. First, treating specialization as a species-level attribute is a simplification. However, we expect intraspecific variation to be small relative to the strong interspecific differences among all birds. Second, specialization would ideally be measured at the finest ecological resolution possible. However, there is no obvious ‘correct’ level of ecological detail at which specialization should be measured, and using higher resolution specialization data will inevitably entail a loss of geographical and taxonomical coverage. Finally, specialization may be confounded by geographical biases in human knowledge; for example tropical species are typically less known than their temperate counterparts. However, birds are by far the best studied taxon and therefore present the least geographical bias. These data limitations are currently unavoidable caveats for a broad-scale view and birds provide a best-case study system.

Auxiliary environmental variables

To estimate richness relative to environmental constraints and to account for the possibility that assemblage-level specialization is driven by patterns of resource availability (Devictor
et al., 2010; Kissling et al., 2011), we extracted key environmental predictors that (1) have been shown to be strong predictors of avian richness gradients, and (2) are directly related to resource availability. Average annual above-ground net primary productivity was estimated using the Lund Potsdam Jena dynamic global vegetation model, which accounts for land use (Bondeau et al., 2007). For the finest scale, we estimated productivity at 1 km resolution using MODIS imagery and the MOD17 algorithm, averaged over the years 2000–2006. We used the number of distinct land-cover types, based on 96-class USGS 1 km resolution GLCC product (http://edc2.usgs.gov/glcc/), as a measure of habitat heterogeneity. All environmental predictors were log_{10}-transformed prior to analyses.

**Analyses**

We predict that specialization will only limit richness when richness is high relative to the local environmental constraints. We tested this by: (1) applying quantile regressions to pinpoint the most diverse assemblages (we used the 0.9 quantile but other high quantiles gave similar results; Fig. S4 in Appendix S1), (2) statistically accounting for environmental variables which may constrain richness (productivity, habitat heterogeneity and, for fine-grained assemblages, area) by including them in a multiple regression framework, and (3) splitting the data into quartiles according to the residuals of a linear model relating species richness to environmental variables. For the latter, we postulate that the richness–specialization relationship will be stronger for higher quartiles, i.e. in assemblages which are richest relative to the environmental constraints.

As both diet and habitat specialization show strong variation and the directionality of the relationship is not straightforward, we used reduced major axis regressions, which are symmetrical, in addition to ordinary least squares. Sample size differences might hinder direct comparison between scales, so we repeated some analyses for the 12,100 km^2 grid using only cells containing fine-grained assemblages. Pseudo-\(R^2\) for quantile regressions was determined as \(1 - \text{sum of weighted distances/sum of weighted distances for an intercept-only model}\). All analyses were performed in R v. 2.13.0 (R Development Core Team, 2011). Quantile regressions were performed using the package ‘quantreg’ (Koenker, 2011) and reduced major axis regressions using the package ‘lmodel2’ (Legendre, 2008).

To account for spatial autocorrelation we also applied simultaneous autoregressive (SAR) models. We used row-standardized SAR spatial error models, examined a range of possible neighbourhood sizes (200–3800 km), and chose the model with the lowest Akaike information criterion (AIC) score. We calculated pseudo-\(R^2\) values for the SAR models as the squared Pearson correlation between observed values and those predicted by the spatial models. Here, \(R^2_{spatial}\) represents the total amount of variance explained by the model, including the spatial component, while \(R^2_{trend}\) represents the amount of variance explained by the non-spatial smooth component alone. Moran’s I global test was used to determine whether residual autocorrelation persisted after fitting the SAR model. The significance of Moran’s I standard deviate was assessed by randomization. SAR analyses were performed using the package ‘spdep’ (Bivand, 2011).

When estimated as the number of habitats within the entire species range, habitat specialization may correlate with range size (e.g. Davies et al., 2009). In this study we reduce this inherent correlation by using independent specialization estimates for each species based on observed habitat utilization. Yet, as a correlation remained (12,100 km^2 grid: \(r = -0.66\), fine-grained assemblages; \(r = -0.72\)) we repeated the analysis using log_{10} mean range size as an additional predictor (Fig. S5 in Appendix S1). Because range size itself is a measure of specialization (specialized species usually have narrow ranges), further attempts to control for range-size variation run the risk of inadvertently controlling for specialization patterns.

To account for sampling effects potentially causing a spurious richness–specialization association, we constructed a null model in which species were randomly drawn from the global species list, weighted by their corresponding range size. This approach preserves local richness and the global species–specialization distribution, but assumes no dispersal limitation. We compared the shape and slope of the null relationship to empirical patterns to determine whether a bounded species–specialization relationship is expected by chance alone.

**RESULTS**

Avian diet and habitat specialization are distributed highly unevenly between species, with many more specialized than generalist species (Fig. 1a). Average values of assemblage specialization show strong variation at each of the three scales of analysis (biome-realm, 12,100 km^2 grid cells and fine-grained assemblages), with a small trend towards higher mean specialization at coarse scales (Fig. 1b–d). Mean assemblage-level avian diet and habitat specialization show distinct geographical and latitudinal variation. Both habitat and diet specialization are highest at low latitudes, decrease towards middle latitudes, and increase again at extremely high latitudes (Fig. 2). Comparing 12,100 km^2 grid cells, mean diet specialization exhibits noticeably high values across South America, much of sub-Saharan Africa, Southeast Asia and parts of Siberia. Habitat specialization also presents clear geographic gradients, with high values most prominently in the Neotropics, Southeast Asia and the Tibetan Plateau and low values across most of the Palaeartic, Australia and southern Africa (Fig. 2).

We find strong geographic similarities between assemblage-level specialization and known richness gradients (Fig. 2). Clear relationship between richness and mean diet and habitat specializations exist at the realm and biome-realm scales (Fig. 3; upper panels). Under a global null model, the relationship between richness and specialization is funnel-
Figure 2 The global distribution of mean (a) dietary specialization, (b) habitat specialization and (c) species richness of terrestrial birds within 12,100 km² grid cells. Points represent fine-grain assemblages. Columns to the left represent means across latitudinal bands using the same colour scale as the maps.
shaped, with large variability at low richness and decreasing variance— but otherwise no trend—with increasing richness (Fig. 3; middle panels, dashed lines). The slopes of the null relationship between richness and specialization are low for both ordinary least squares (OLS) [Diet: 0.0 (−0.10–0.11 95% confidence interval (CI)); habitat, −0.02 (−0.06–0.01)] and 0.9 quantile regressions [diet: 0.0 (−0.13–0.14); habitat, 0.01(−0.10–0.10)]. This contrasts strongly with empirical patterns for 12,100 km² grid cells, which above c. 100 species richness becomes increasingly restricted from above at low values of specialization (Fig. 3; middle panels) creating a positive richness–specialization relationship [OLS: diet 0.80 ± 0.01 (SE), habitat 0.22 ± 0.01; 0.9 quantile regression: diet 0.81 ± 0.01, habitat 0.30 ± 0.01]. The 0.9 quantile regression slopes are steeper for the 12,100 km² scale than for the fine-grained assemblages [significant interaction between the two-level categorical predictor scale (12,100 km² grid and fine-grained assemblages) and specialization as a continuous predictor; for habitat: t value (P) = 3.75 (< 0.001); for diet: 5.46 (< 0.001)]. Strong richness–specialization associations are also found within individual realms (Fig. 3; lower panels).

We predicted that richness–specialization associations would remain strong, even after accounting for gradients in environmental resource availability. Our analyses confirm previous evidence that proxies for broad-scale gradients in resource availability, such as net primary productivity and habitat heterogeneity, are strong predictors of species richness (Table 1). However, additionally fitting both diet and habitat specialization in a multi-predictor setting reveals strong, complementary and positive effects on richness, especially at the 12,100 km² grid scale (Table 1). The richness–specialization relationship also remains strong when using major axis regressions (Table 2), which are symmetrical and thus do not assume any cause and effect relationship.

To assess these associations in more detail, we separate assemblages according to the residuals of the richness–environment (productivity, habitat heterogeneity and area) relationship. Large positive residuals represent particularly species-rich assemblages given environmental conditions, and

Figure 3 The relationship between global terrestrial bird species richness and diet and habitat specialization. (a, b) The relationships across realms and biome-realms. Lines represent ordinary least square regressions. (c, d) Black points represent fine-grained assemblages; coloured dots 12,100 km² grid cells (darkness increases with dot density). Regression lines represent 0.9 quantile regression estimates (12,100 km² grid: pseudo-\(R^2 = 0.32, 0.20\); coefficient = 0.94, 0.31; fine-grained assemblages: pseudo-\(R^2 = 0.24, 0.12\); coefficient = 0.54, 0.18; for diet and habitat specialization, respectively); \(P < 0.001\) in all cases. Regions defined by the dashed lines represent the 95% confidence interval of the null expectation (see Materials and Methods). Regression lines at the 12,100 km² scale are plotted using only grid cells in which fine-grained assemblages are located to maintain sample size for direct comparison. (e, f) Richness–specialization associations for 12,100 km² grid cells within each of the major realms. Lines represent 0.9 quartile regressions (solid lines correspond to significant slopes). Only assemblages with > 100 species were included.
Habitat specialization (Habitat spec., net primary productivity, habitat heterogeneity (Habitat heter.) and, for fine-grained assemblages only, area. Neighbourhood sizes used for the SAR models were 3000, 200 and 1400 km for the biome-realm, 12,100 km² grid and fine-grained habitat specialization (Diet spec.).

**DISCUSSION**

We demonstrate that, for an entire large clade across spatial scales, specialization and species richness are strongly related. Importantly, specialization remains positively associated with richness even after accounting for known environmental correlates of richness, such as productivity. Our results suggest that avian dietary and habitat specialization set upper bounds on species richness, indicating that high richness values are not attained in generalist assemblages (Fig. 2). Conversely, species-rich assemblages are more likely to contain specialized species than assemblages that are species-poor. These findings contradict several recent studies (Vázquez & Stevens, 2004; Novotny et al., 2006) and suggest that the contribution of specialization to global richness gradients may need to be carefully reassessed, taking into consideration the grain, extent and resolution of specialization categorization.

We would like to emphasize that if species richness and specialization were not linked, but rather both associated with areas containing more habitats or dietary types, we would expect a negative, not a positive, relationship between specialization and richness. Simple random sampling of the environment would cause species to have wider diets and use more habitats in heterogeneous and therefore species-rich areas. Similarly, species would be habitat and diet specialists in localities with limited diet or habitat options (e.g. few diet categories used in cold or high-elevation regions might reflect limitations of available feeding strategies). However, we find the opposite pattern: an increase in specialization with richness, which is more consistent with our expectation.

We find that the relationship between specialization and species richness is steep even at coarse scales (realm and biome-realm) and steeper for the 12,100 km² scale than for fine-grained assemblages. If the observed associations between richness and specialization were simply the result of contemporary ecological filters (e.g. those precluding non-specialists from entering local assemblages), we would expect to observe shallower relationships at coarse scales. The same argument holds also when viewing a reverse direction of causality. If competition for limited local resources causes species in diverse regions to specialize, we would predict shallower richness-specialization associations at coarse scales where resource partitioning is not a major limitation. Instead, it appears that the positive richness-specialization relationship is

**Table 1** Multi-predictor models of species richness in terrestrial birds (9061 species) globally. Ordinary least squares, quantile (0.9 quantile) and simultaneous autoregressive (SAR) regressions are presented. For all regressions, predictors included diet specialization (Diet spec.), habitat specialization (Habitat spec.), net primary productivity, habitat heterogeneity (Habitat heter.) and, for fine-grained assemblages only, area.

<table>
<thead>
<tr>
<th>Scale</th>
<th>Variable</th>
<th>Coef. (SE)</th>
<th>t value</th>
<th>Coef. (SE)</th>
<th>t value</th>
<th>Coef. (SE)</th>
<th>z value</th>
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<tr>
<td>Biome-Realm</td>
<td>Habitat spec.</td>
<td>0.27 (0.16)</td>
<td>1.6</td>
<td>0.24 (0.15)</td>
<td>1.6</td>
<td>0.63 (0.15)</td>
<td>4.1***</td>
</tr>
<tr>
<td></td>
<td>Diet spec.</td>
<td>0.50 (0.29)</td>
<td>1.7</td>
<td>0.93 (0.40)</td>
<td>2.4*</td>
<td>0.27 (0.36)</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td>Productivity</td>
<td>0.09 (0.14)</td>
<td>0.6</td>
<td>-0.18 (0.16)</td>
<td>-1.14</td>
<td>-0.06 (0.12)</td>
<td>-0.5</td>
</tr>
<tr>
<td></td>
<td>Habitat heter.</td>
<td>0.32 (0.27)</td>
<td>1.2</td>
<td>0.26 (0.28)</td>
<td>0.92</td>
<td>0.28 (0.26)</td>
<td>1.0</td>
</tr>
<tr>
<td></td>
<td><strong>Summary:</strong></td>
<td>R²_adj = 0.37, P &lt; 0.001</td>
<td>R²_Pseudo = 0.47, P &lt; 0.001</td>
<td>R²_trend = 0.36, R²_fie = 0.58</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>12,100 km² grid</td>
<td>Habitat spec.</td>
<td>0.05 (0.03)</td>
<td>7.8***</td>
<td>0.08 (0.01)</td>
<td>11.1***</td>
<td>0.18 (0.01)</td>
<td>29.8***</td>
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<tr>
<td></td>
<td>Diet spec.</td>
<td>0.54 (0.01)</td>
<td>41.***</td>
<td>0.52 (0.01)</td>
<td>37.1***</td>
<td>0.04 (0.01)</td>
<td>3.9***</td>
</tr>
<tr>
<td></td>
<td>Productivity</td>
<td>0.22 (0.00)</td>
<td>58.***</td>
<td>0.17 (0.01)</td>
<td>27.0***</td>
<td>0.07 (0.00)</td>
<td>25.6***</td>
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<tr>
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<td>Habitat heter.</td>
<td>0.19 (0.01)</td>
<td>20.***</td>
<td>0.16 (0.01)</td>
<td>13.7***</td>
<td>0.05 (0.00)</td>
<td>17.4***</td>
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<td></td>
<td><strong>Summary:</strong></td>
<td>R²_adj = 0.60, P &lt; 0.001</td>
<td>R²_Pseudo = 0.43, P &lt; 0.001</td>
<td>R²_trend = 0.41, R²_fie = 0.99</td>
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<td>Fine-grained</td>
<td>Habitat spec.</td>
<td>-0.00 (0.03)</td>
<td>-0.15</td>
<td>-0.03 (0.02)</td>
<td>-1.6</td>
<td>-0.01 (0.04)</td>
<td>-0.3</td>
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<tr>
<td></td>
<td>Diet spec.</td>
<td>0.21 (0.06)</td>
<td>3.5***</td>
<td>0.55 (0.06)</td>
<td>8.8***</td>
<td>0.31 (0.07)</td>
<td>4.1***</td>
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<tr>
<td></td>
<td>Productivity</td>
<td>0.18 (0.03)</td>
<td>6.9***</td>
<td>0.17 (0.02)</td>
<td>9.0***</td>
<td>0.16 (0.03)</td>
<td>5.6***</td>
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<tr>
<td></td>
<td>Habitat heter.</td>
<td>0.03 (0.05)</td>
<td>0.7</td>
<td>0.07 (0.03)</td>
<td>2.1*</td>
<td>0.06 (0.05)</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>Area</td>
<td>0.03 (0.02)</td>
<td>1.7</td>
<td>0.01 (0.01)</td>
<td>0.6</td>
<td>0.02 (0.02)</td>
<td>1.3</td>
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<tr>
<td></td>
<td><strong>Summary:</strong></td>
<td>R²_adj = 0.21, P &lt; 0.001</td>
<td>R²_Pseudo = 0.33, P &lt; 0.001</td>
<td>R²_trend = 0.21, R²_fie = 0.27</td>
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Coef., coefficient; *, P < 0.05; ***, P < 0.001. Significant (P < 0.05) relationships are italicized and marked in bold.
Table 2 The relationship between specialization and species richness in 9061 terrestrial bird species globally. Single-predictor analyses are presented in which the response is species richness and the predictor is either habitat or diet specialization. For the 12,100 km² grid and fine-grained assemblages, data were partitioned and analyzed separately for different quartiles (small sample size prevented this for the coarser scales). Quartile delineation was derived from first relating species richness to environmental variables (productivity, habitat heterogeneity and, for fine-grained assemblages, area) and then separating the assemblages according to the residuals of this model. Quartiles range from first (lowest 25% residuals) to fourth (highest 25% residuals).

<table>
<thead>
<tr>
<th>Scale</th>
<th>Specialization</th>
<th>Quartiles</th>
<th>RMA Coef. (95% CI)</th>
<th>OLS Coef. (SE)</th>
<th>t value</th>
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</thead>
<tbody>
<tr>
<td>Realm</td>
<td>Habitat spec.</td>
<td>all</td>
<td>0.6 (–0.2–3.2)</td>
<td>0.5 (0.3)</td>
<td>1.9</td>
</tr>
<tr>
<td></td>
<td>Diet spec.</td>
<td>all</td>
<td>1.4 (0.7–3.6)</td>
<td>1.2 (0.3)</td>
<td>3.9*</td>
</tr>
<tr>
<td>Biome-Realm</td>
<td>Habitat spec.</td>
<td>all</td>
<td>0.8 (0.6–1.2)</td>
<td>0.5 (0.1)</td>
<td>5.5***</td>
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<tr>
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<td>Diet spec.</td>
<td>all</td>
<td>2.2 (1.6–3.6)</td>
<td>0.9 (0.2)</td>
<td>5.1***</td>
</tr>
<tr>
<td>12,100 km² grid</td>
<td>Habitat spec.</td>
<td>1</td>
<td>0.77 (0.74–0.80)</td>
<td>0.19 (0.01)</td>
<td>12.8***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.60 (0.58–0.62)</td>
<td>0.04 (0.01)</td>
<td>3.0**</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>0.80 (0.77–0.83)</td>
<td>0.16 (0.02)</td>
<td>9.9***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>0.68 (0.65–0.70)</td>
<td>0.33 (0.01)</td>
<td>27.8***</td>
</tr>
<tr>
<td></td>
<td>Diet spec.</td>
<td>1</td>
<td>1.70 (1.64–1.76)</td>
<td>0.76 (0.03)</td>
<td>25.1***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>1.40 (1.34–1.45)</td>
<td>0.21 (0.03)</td>
<td>7.9***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>1.89 (1.79–1.92)</td>
<td>0.81 (0.03)</td>
<td>24.4***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>1.54 (1.50–1.59)</td>
<td>1.02 (0.02)</td>
<td>43.8***</td>
</tr>
<tr>
<td>Fine-grained</td>
<td>Habitat spec.</td>
<td>1</td>
<td>0.38 (0.31–0.47)</td>
<td>0.02 (0.04)</td>
<td>0.6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>0.20 (0.17–0.25)</td>
<td>0.01 (0.02)</td>
<td>0.7</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>0.20 (0.16–0.24)</td>
<td>0.05 (0.02)</td>
<td>2.7***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>0.30 (0.25–0.36)</td>
<td>0.13 (0.03)</td>
<td>4.9***</td>
</tr>
<tr>
<td></td>
<td>Diet spec.</td>
<td>1</td>
<td>0.63 (0.52–0.76)</td>
<td>0.24 (0.06)</td>
<td>4.1***</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2</td>
<td>–0.42 (–0.52–0.35)</td>
<td>–0.02 (0.04)</td>
<td>–0.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3</td>
<td>0.53 (0.44–0.64)</td>
<td>0.18 (0.05)</td>
<td>3.6***</td>
</tr>
<tr>
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<td></td>
<td>4</td>
<td>0.75 (0.65–0.87)</td>
<td>0.51 (0.05)</td>
<td>9.1***</td>
</tr>
</tbody>
</table>

Coef., coefficient; Diet spec., diet specialization; Habitat heter., habitat heterogeneity; Habitat spec., habitat specialization; *, P < 0.05; **, P < 0.01; ***, P < 0.001. Significant (P < 0.05) relationships (for ordinary least squares regression; OLS) or slopes with 95% confidence intervals (CI) excluding zero (for reduced major axis regression; RMA) are italicized and marked in bold.

shaped by regional evolutionary processes, which are expressed from regional to fine grains (Ricklefs, 2008). For example, the large radiation of the Furnariidae and Tyrannidae families (Irestedt et al., 2006; Ohlson et al., 2008), which have relatively narrow dietary niches, exerts a signal on the high dietary specialization of the South American assemblages (Fig. 2).

Studies conducted at a global extent are limited by the coarseness of the available distribution data, which applies to specialist species even more than generalist species (Jetz et al., 2008). By including relatively fine-grained assemblages we show that, down to a grain equivalent to c. 22 × 22 km grid cells (median fine-grain assemblage size was 488 km²), the richness–specialization slope does not steepen. This suggests that any signature of local resource partitioning on assemblage-level specialization may be weak, or may be most apparent at yet finer scales.

Although the richness–specialization relationship is strong and consistent in shape across realms, considerable scatter remains, and a wide range of richness values can be found at each specialization level (Fig. 3), even after accounting for environmental conditions (Table 1). In this study, specialization estimates were obtained using relatively coarse resolution data and it is probable that most species can differentiate finer habitat and diet delimitations. However, even a warbler that distinguishes between different microhabitats in a single tree (MacArthur, 1958), may use both a montane and a lowland forest (see categories in Appendix S2). Therefore, it is unclear what habitat and diet resolutions are the most appropriate. Nevertheless, using coarse habitat and diet categorizations, which are likely to be strongly conserved phylogenetically, could have contributed to the large variability in the richness–specialization associations. Stronger associations may be uncovered by using more detailed specialization data acquired at finer scales.

Specialization should ideally be measured by comparing observed resource utilization with resource availability at the same geographic location. However, dietary resources and fine-grained habitats are not available globally and therefore, in practice, such standardization is rarely performed (Vázquez & Stevens, 2004). Here, we use habitat variety and net primary productivity as proxies for habitat and diet availability. The strong and positive influence of specialization on richness was evident even after accounting for these gradients in resource availability (Table 1). Therefore, the richness–specialization association does not simply mirror well-established environmental gradients. Productivity, in particular, has been
suggested to promote specialization (MacArthur, 1965; Evans et al., 2006), and hence may be a confounding factor when analysing richness–specialization associations. This study demonstrates that specialization has an independent contribution to richness above and beyond that attributed to productivity. Hence, and assuming richness is casually linked to specialization, gradients in resource availability (manifested as more habitats or energetic niches, Hurlbert, 2004; Anderson & Jetz, 2005; Clarke & Gaston, 2006; Novotny et al., 2006; Belmaker, 2009; Kissling et al., 2011) may operate in tandem with gradients in specialization to establish richness patterns.

Range size is in itself a measure of specialization (Stevens, 1989; Jocque et al., 2010). It is thus difficult to control for range-size variation without running the risk of inadvertently controlling for specialization patterns. Nevertheless, diet and habitat specialization remain independent contributors to richness, even after accounting for geographic variation in range size (Fig. S5 in Appendix S1). Therefore, the richness–specialization relationship does not solely reflect known geographic variation in range sizes, most notably the decrease in range size towards low latitudes (Stevens, 1989). Wide-ranged species contribute disproportionally to richness gradients (Jetz & Rahbek, 2002). In accordance, we find that the richness–specialization relationship is strongest for the 50% most wide-ranged species (Fig. S6 in Appendix S1). This suggests that much of the global relationship may be attributed to the replacement of wide-ranged generalists in species-poor regions by wide-ranged specialists in species-rich regions.

The positive but largely coarse-scale association between richness and specialization supports several, not mutually exclusive, hypotheses. First, specialization might facilitate the origination of high-diversity assemblages, in addition (or instead) of an effect on contemporary assembly. For example, specialization may promote high diversification rates by increasing reproductive isolation between populations (Hawthorne & Via, 2001; Jocque et al., 2010). In addition, a positive richness–specialization relationship may form over evolutionary time and at coarse geographical scales if specialization increases the effectiveness of resource use, consequently reducing the within-clade ecological limits on diversification (Phillimore & Price, 2008; Rabosky, 2009). In both of these examples a positive assemblage-level richness–specialization relationship emerges due to intrinsic differences among clades in diversification rates and may thus be independent of local environmental constraints (although the environment may strongly influence specialization levels; Jocque et al., 2010). This is in line with our results, which reveal only limited support for context-dependence in the richness specialization association, as we do not find an increase in the steepness of the richness–specialization relationship at higher quartiles of richness–environment residuals.

A second explanation for the positive richness–specialization relationship is that the association between the two is in fact not causal, but that instead both are linked independently to a third variable. We find the richness–specialization association to be independent of prominent environmental gradients (notably productivity), but it is impossible to exclude the possibility that unmeasured environmental variables or life-history traits affect both specialization and richness.

Finally, the direction of causality may in fact be reversed and the positive richness–specialization relationship primarily brought about by richness influencing patterns of specialization. Diverse assemblages may be more likely than species-poor assemblages to coevolve towards increased specialization (MacArthur, 1965; Rosenzweig & Ziv, 1999). However, we expect such a pattern to be largely confined to fine scales where competition for limited resources, postulated to drive such a process, should be strongest. It has also been suggested that asymmetrical interaction networks, where specialists tend to interact with generalists, can cause a positive correlation between specialization and richness (Vázquez & Stevens, 2004). However, here too we may expect the pattern to be most pronounced at fine scales where species interactions take place. We cannot currently envision a mechanism by which higher species richness will cause gradients in specialization primarily at coarse scales. Nevertheless, lacking fully resolved phylogenetic trees and data on the past occurrences and interactions of species, we are unable to directly quantify the effect of regional diversity on the evolution of specialization across clades. Thus, the goal of this study was a first geographic assessment and a general test of ideas regarding niche-partitioning and community assembly. Separating the directionality of effects will require further research that may need to be limited in geographic and taxonomic scope.

In conclusion, we demonstrate that globally high bird species richness is positively associated with specialization. We interpret our findings across scales as indicating a relatively minor role for niche-partitioning mechanisms in causing this pattern. We suggest that our results support a regional and evolutionary perspective for understanding how specialization is associated with global geographic gradients in species richness.

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**SUPPORTING INFORMATION**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Additional figures detailing the relationship between specialization and species richness of birds of the world (Figs S1–S6).

**Appendix S2** Summary of the IUCN assessment habitat categories.

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