LETTER

The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds

Claire L. Salisbury, Nathalie Seddon, Christopher R. Cooney, and Joseph A. Tobias*

Edward Grey Institute, Department of Zoology, University of Oxford, South Parks Road, Oxford, OX1 3PS, UK

*Correspondence: E-mail: joseph. tobias@zoo.ox.ac.uk

Abstract

Physiological and behavioural constraints arising from ecological specialisation are proposed to limit gene flow and promote diversification in tropical lineages. In this study, we use phylogenetic analyses to test this idea in 739 Amazonian bird species. We show that patterns of species and subspecies richness are best predicted by a suite of avian specialisms common in tropical avifaunas but rare in the temperate zone. However, this only applied to niche traits associated with dispersal limitation rather than vagility. These findings are consistent with the view that diversity is promoted by more finely partitioned niches, although not simply by coevolutionary adaptation and niche packing as is often assumed. Instead, they suggest that diversification is driven by dispersal constraints, and that niches characterised by these constraints are biased towards tropical systems. We conclude that specialised tropical niches reduce the likelihood of dispersal across barriers, thereby increasing allopatric diversification and contributing to the latitudinal diversity gradient.

INTRODUCTION

The latitudinal diversity gradient (LDG) of increasing species richness towards the equator is almost ubiquitous (Rohde 1992; Hillebrand 2004), yet the underlying processes causing this pattern remain poorly understood (Mittelbach *et al.* 2007). Most studies have focused on the potential role of extrinsic factors, such as temperature, rainfall and productivity, many of which predict biological diversity (Hawkins *et al.* 2003). However, these associations are all highly correlated with latitude, and tell us little about the mechanisms driving the LDG (Mittelbach *et al.* 2007).

One possibility is that macroecological patterns have occurred without the need for latitudinal variation in diversification mechanisms. Thus, the build up of tropical diversity may simply arise through historical and geographical contingency, particularly as the tropics offer larger areas for speciation, and support older clades with lower extinction rates (Colwell & Lees 2000; Wiens *et al.* 2011). Alternatively, patterns of diversity may reflect extrinsic biotic processes. It has long been proposed, for example, that tropical climates give rise to greater structural complexity in habitats, which in turn provides more niches (MacArthur 1964). This hypothesis is based on the idea that niche packing allows a greater number of species to coexist along any particular niche axis, increasing the potential for tropical diversification. However, the role of niche width in shaping the LDG remains unclear, partly because most studies have focused on examining correlations with latitude rather than pinpointing causality (e.g. Vázquez & Stevens 2004). As niche packing may theoretically occur long after speciation, the extent to which niches are finely partitioned says little, if anything, about the mechanisms driving diversification.

Although most attention has focused on purely extrinsic factors, it is possible that key diversification mechanisms operating in the tropics have important intrinsic components. In other words, the fundamental differences between tropical and temperate biotas may relate to evolutionary processes and interactions (Dobzhansky 1950; Mittelbach *et al.* 2007). It has been proposed, for example,

that higher temperatures in equatorial regions may accelerate molecular evolution and mutation, thereby increasing rates of speciation (Rohde 1992). Similarly, the relative stability of tropical environments is thought to increase the specialism of biotic interactions, such as mutualisms and antagonisms, potentially driving rapid adaptation and speciation via coevolutionary processes (Schemske *et al.* 2009). Both these mechanisms could operate in sympatry or geographical isolation, but the evidence in either case is often inconclusive (Mittelbach *et al.* 2007; Schemske *et al.* 2009).

An alternative mechanism was proposed by Janzen (1967), who argued that tropical taxa are adapted to more stable climates than their temperate-zone equivalents, and thus have narrower physiological tolerance of variation in temperature. He suggested that organisms occurring in the tropics were therefore subject to stronger barrier effects, using the example of montane species unable to cross climatic gradients. In its original form, this model was not specifically linked to diversification, but it is clear that greater subdivision of populations could promote allopatric speciation, providing an evolutionary mechanism for higher tropical species richness. It differs from other such mechanisms because it applies exclusively to the division of populations into allopatric subpopulations, and is not dependent on rapid mutation, adaptation or coevolution.

Janzen's model is now supported by a range of evidence from the montane tropics (Ghalambor *et al.* 2006; Kozak & Wiens 2007; McCain 2009; Cadena *et al.* 2011). However, it generates few predictions about patterns of diversity across taxonomic groups, as it lacks a conceptual connection to species ecology. Moreover, it does little to illuminate diversification processes in tropical lowlands, where there is effectively no climatic gradient (Wright *et al.* 2009) and yet species richness is often higher. This implies that climatic niche stratification offers only a partial explanation for the LDG, and that the search for underlying biotic mechanisms should include more general processes linked to ecological niches.

One recent proposal is that a trade-off between dispersal ability and ecological specialisation can explain patterns of diversification

(Jocque *et al.* 2010). This idea contrasts with Janzen's hypothesis in that it does not rely on climatic niche constraints but on the role of stable climates in promoting the evolution of narrow ecological niches – thus shifting the focus from physiology to all aspects of ecology, including diets, microhabitats, and behaviours. Jocque *et al.* (2010) argue that the kinds of local adaptation promoted by climatic stability select for reduced dispersal, and therefore increased allopatric speciation in tropical organisms. This framework does not depend on divergence in ecological niches, and is thus fundamentally different from 'adaptive radiation' or 'ecological speciation' (see Wiens 2004; Rundell & Price 2009). It offers a universal mechanism behind the LDG because climatic seasonality at higher latitudes is predicted to select for greater dispersal ability, resulting in higher levels of gene flow and fewer opportunities for speciation (Dynesius & Jansson 2000; Jocque *et al.* 2010). However, it lacks empirical support, particularly in tropical systems where the link between specialism and diversification is not firmly established (Vázquez & Stevens 2004; Novotny *et al.* 2006).

Birds are a useful case study because they are highly variable in dispersal ability and ecological specialisation. In a global analysis, dietary generalism and high annual dispersal emerged as the strongest predictors of avian diversification rate (Phillimore *et al.* 2006), apparently contradicting the dispersal-specialisation trade-off hypothesis. At a more regional scale, ecological traits associated with low dispersal were positively associated with diversification (Belliure *et al.* 2000; Burney & Brumfield 2009; Claramunt *et al.* 2012). These contrasting findings suggest that different mechanisms may operate within different scales and contexts. In addition, they highlight the need for further analyses because previous studies are not able to tease apart the effects of long-distance colonisation events (Phillimore *et al.* 2006) or thermal intolerance to intervening climates (Burney & Brumfield 2009).

We addressed these issues by evaluating the relationship between specialism and diversification in Amazonian birds. This region provides an ideal system for understanding macroecological patterns for two reasons. First, it supports the highest levels of alpha diversity found in any terrestrial ecosystem, and over 15% of the global avifauna (Vale *et al.* 2008). Thus, processes operating within Amazonia play a major role in shaping the LDG. Second, it is relatively homogenous in topography and climate (Wright *et al.* 2009), so the climatic niche constraints proposed by Janzen (1967) are unlikely to play a dominant role. Instead, most models of Amazonian diversity rely on abiotic correlations or vicariance. The former point to the role of geological history and nutrient supply (Hoorn *et al.* 2010), or the sheer length of time for speciation since colonisation events (Wiens *et al.* 2011). The latter rely on allopatric speciation mediated by low dispersal between putative forest refugia (Haffer 1997) or across major rivers (Wallace 1852; Ribas *et al.* 2011).

The potential importance of dispersal constraints in driving the build-up of Amazonian diversity allows us to test a central prediction of Jocque *et al.*'s hypothesis: the positive relationship between ecological specialisation and diversification in tropical systems. We assessed diversity using the standard metric of species richness. Focusing at this taxonomic level enables a preliminary assessment of niche-related traits and diversity, but it has important limitations. Most significantly, a link between specialisation and diversity may simply reflect the fact that narrow niches allow more species to pack into a given community, and does not identify how those species arose. Moreover, it is not certain that current ecological

niches match ancestral traits involved in historical diversification events, particularly as numerous species may have colonised the region from elsewhere (e.g. Brumfield & Edwards 2007).

To provide a more direct test of niche-related drivers of allopatric diversification we also used subspecies richness as an index of diversity, following recent studies of avian diversification (e.g. Phillimore *et al.* 2007; Martin & Tewksbury 2008; see Appendix S1). Avian subspecies are less likely than species to represent units of neutral genetic diversity (Zink 2004), but they nonetheless offer useful insight into processes underlying recent diversification (Phillimore & Owens 2006; Phillimore 2010; Winker 2010). The benefits of using subspecies are twofold. First, their younger age in relation to species minimises the influence of broader historical or biogeographical processes. Second, they are by definition always allopatric, which means that the accumulation of diagnostic subspecies is typically dependent on current barriers to gene flow within the study region. Focusing on subspecies therefore allows us to step beyond MacArthur's (1964) niche packing hypothesis, and to investigate key mechanisms relevant to allopatric diversification in the tropics.

The main advantages of investigating this question in birds is the availability of taxonomic and geographical range data, as well as background information on ecological traits, and genetic sequences to determine phylogenetic relationships. We take advantage of these resources by testing the role of specialisation in diversification using a mixed modelling framework with phylogenetic correction. In addition, the existence of contrasting behaviours with different implications for dispersal-specialisation dynamics – for example, long-distance food tracking by specialist frugivores vs. year-round territoriality by specialist insectivores (Levey & Stiles 1992; Burney & Brumfield 2009), or gap-crossing canopy species vs. gap-averse understorey species (Harris & Reed 2002; Stratford & Robinson 2005) – allows us to ask whether the key driver of diversification is related primarily to specialism, dispersal or a combination of both.

MATERIALS AND METHODS

Study species, range data and endemicity

We defined Amazonia as the region below 500 m elevation extending from the Orinoco and Meta rivers in Venezuela, west to the base of the Andes, east to the Atlantic, and south to the edge of rainforest in Bolivia and Brazil (Stotz *et al.* 1996). To focus on processes within this region, we excluded all species breeding primarily in non-forested habitats (i.e. wetlands, grasslands and urban areas), or visiting only in the non-breeding season. For all species, range sizes were taken from a global database of breeding distributions, or (in 45 cases) generated using ArcMap 10 (see Appendix S1). The final dataset contained 739 bird species, spanning 45 families (1–121 species each, mean = 16.42) and 313 genera (1–17 species each, mean = 2.36). Roughly half of these lineages (385 species; 52%) were endemic to Amazonia.

Taxonomic richness

We defined species richness as the number of species within genera, and subspecies richness as the number of currently recognised subspecies (per species) with part or all of their range within Amazonia. Our final dataset contained 1366 subspecies, an average of 1.85 subspecies per species (Table S2). The view of subspecies as meaning-

ful units (see above) may apply particularly well to Amazonia, where many intraspecific lineages appear to be cryptic or incipient species geographically isolated by major rivers (Tobias *et al.* 2008; Ribas *et al.* 2011). To examine the temporal context of subspeciation in this region, and to test whether subspecies richness is a valid proxy for recent diversification, we used genetic sequence data to estimate the time since cladogenesis for a sample of Amazonian sister species (Table S5) and subspecies (Table S6). See Appendix S1 for full phylogenetic and statistical methods, and detailed discussion of the utility of subspecies in studies of diversification.

Ecological trait data

For each species, we quantified variation in a suite of ecological niches: habitat, forest type, foraging strata, diet and territorial system. These variables are all theoretically related to dispersal ability or dispersal likelihood in an Amazonian context. Following previous studies of diversification (e.g. Burney & Brumfield 2009), ecological data were collated from Stotz *et al.* (1996), with updates and amendments from additional sources (Tables S1 and S2; for expanded methods and rationale see Appendix S1).

To quantify habitat specialisation, we counted the number of preferred habitats listed per species by Stotz *et al.* (1996) and produced a categorical variable with two levels: (1) habitat generalist (occurring in $\geq$ 2 habitat types) and (2) habitat specialist (occurring in one habitat type). To quantify forest-type specialisation, we assigned species to one of three categories: (1) occurring in upland and floodplain forest, (2) floodplain specialist (exclusively associated with rivers) and (3) upland specialist (exclusively associated with *terra firme* rather than riverine or flooded forest). To quantify foraging strata specialisation, we assigned species to one of three categories: (1) strata generalist (found in > 1 strata), (2) canopy specialist (restricted to the canopy and/or subcanopy) and (3) understorey specialist (restricted to the forest floor or understorey).

We also compiled data on dietary and behavioural specialisms. Species were assigned to one of three dietary categories representing their primary adult food source; (1) omnivore (more than one type of major food source), (2) non-insectivore specialist and (3) insectivore specialist. Almost all non-insectivorous species were frugivores, but this category also includes small numbers of nectarivores, carnivores and piscivores. To quantify territorial behaviour, we assigned species to one of two categories: (1) seasonal, mixed-flock or non-territorial or (2) year-round territorial (i.e. spatially fixed pair or group territories held during all seasons). We extracted this information from a range of sources, including personal data, online archives and primary literature (see Appendix S1, Table S1–S2).

Comparison between specialists and generalists

To examine the relationship between traits and diversification, we modelled the effects of ecological specialisation on both species and subspecies richness using a Bayesian approach (see below). We ran species-level models corrected for taxonomy, and genus-level models with full phylogenetic correction. These different approaches were necessary because phylogenetic data were available at the level of genus, but not species. Both types of model compared species and subspecies richness of specialists vs. generalists. Contrasting specialisms (e.g. understorey and canopy specialism) were pooled together

under one category ('specialists') to test the link with diversification proposed by Jocque *et al.* (2010).

Comparison between alternative specialisms

To test the importance of dispersal, we used the same modelling approaches to compare species and subspecies richness between different specialist niches with contrasting associations with dispersal ability. We ignored habitat and territoriality as these were difficult to partition in relation to alternative specialisms. Instead, we focused on non-overlapping points along three major niche axes: forest type (floodplain specialist; upland specialist), foraging strata (canopy specialist; understorey specialist), and diet (non-insectivore specialist; insectivore specialist). In each case, the first option implies higher likelihood of dispersal across riverine barriers (Hayes & Sewlal 2004; Moore *et al.* 2008; Burney & Brumfield 2009; see Appendix S1). For genus-level models, we first calculated the proportion of species within each genus assigned to a particular specialism, and assigned the genus to that specialism if the proportion exceeded 0.5. Genera were excluded from analysis if there was an equal split between classifications. Most genera contain either all specialists (1) or all non-specialists (0), so our results are unlikely to be sensitive to the 0.5 threshold (see Figure S2).

To investigate the role of ecology in patterns of species diversification within Amazonia, we compared the total number of species contributed by the same alternative specialisms (floodplain vs. upland; canopy vs. understorey; non-insectivore vs. insectivore). As lineages with multiple specialisms are perhaps most likely to speciate, we also compared diversity associated with multiple low-dispersal niches (understory insectivores) against multiple high-dispersal niches (canopy frugivores). We then used chi-squared analyses to test whether low-dispersal niches (or multiple niches) contribute disproportionately to endemic species richness.

Latitudinal patterns

As a preliminary assessment of the potential for specialism-mediated diversification outside the tropics, we compiled ecological data for all breeding bird species (N = 193) occurring in forested habitats in continental North America (USA and Canada; Table S3). Each taxon was assigned to ecological categories following the approach described for Amazonian species, using detailed accounts published in Birds of North America (www.birds.cornell.edu). We omitted habitat and forest type specialisms as these were not directly comparable between tropical and temperate avifaunas. We also treated all long-distance migrants (N = 96) as non-specialists because migratory behaviour is unlikely to be associated with dispersal constraints. Our final dataset contained three non-migratory specialisms: (1) restriction to understorey, (2) specialist insectivory and (3) year-round territoriality. We acknowledge that these traits may have different implications for dispersal in the tropics vs. the temperate zone, and that any comparison needs to be interpreted cautiously. However, a provisional comparison is justified given that each of our target specialisms is associated with reduced vagility regardless of latitude (Harris & Reed 2002; see Appendix S1). To test whether there are differences in the relative contributions of these key specialisms to tropical and temperate biotas, we used chi-square tests comparing the proportion of specialist species in North America and Amazonia.

Statistical analyses

We modelled the effect of ecological specialisation using Markov chain Monte Carlo estimation implemented with 'MCMCglmm' (Hadfield 2010). First, we ran species-level multi-predictor Bayesian Mixed Models (BMMs) to examine the relationship between ecological specialisation and subspecies richness. As genetic sequence data were lacking for many Amazonian species, we applied phylogenetic correction by including taxonomy (i.e. family [genus]) as a nested random effect. Then we ran genus-level Bayesian Phylogenetic Mixed Models (BPMMs) using a multilocus phylogenetic framework

(Fig. 1; see Appendix S1 for phylogenetic methods). BPMMs were used to assess the relationship between the proportion of species within genera that were ecological specialists, and the taxonomic diversity – that is, species and subspecies richness – of the same genera.

We used species and subspecies richness rather than diversification rate (log(N)/t) as response variables because dividing log richness by time assumes a constant rate of diversification, which may not be valid (Rabosky 2009; Phillimore 2010; see Appendix S1). However, comparing across clades on the basis of richness can be problematic if clade age influences diversity, so we used a Spearman
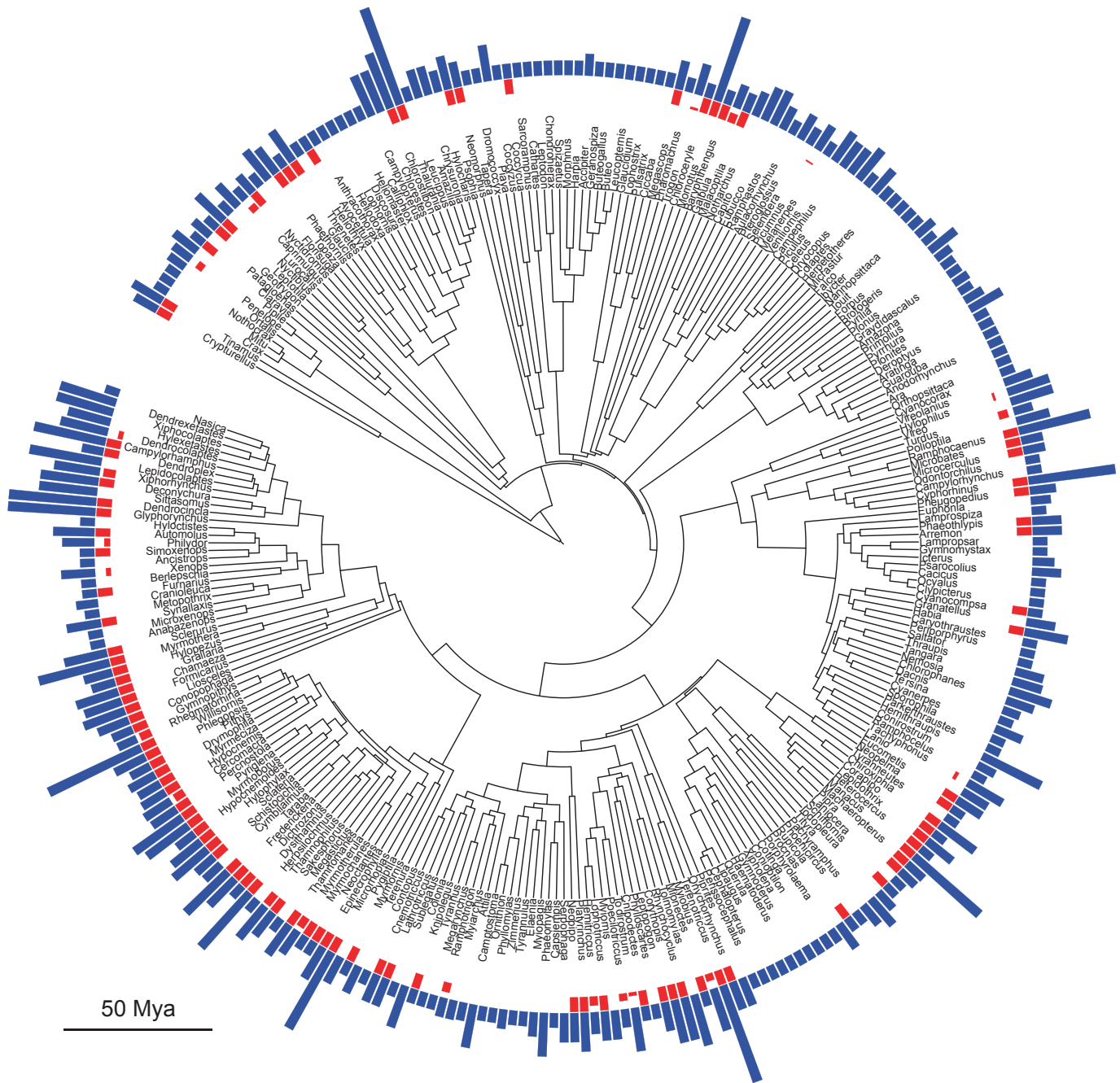

Figure 1 Maximum clade credibility phylogenetic tree illustrating evolutionary relationships between 283 avian genera occurring in Amazonian forests (representing 694 study species). Coloured bars show the association between subspecies richness (blue: mean number of subspecies per species, averaged across the genus) and proportion of species classified as understorey specialists (red).

rank correlation to examine whether species richness (and subspecies richness averaged across all species in a genus) was related to the root age of genera. It was not possible to include species age in our models because phylogenetic data were lacking for many lineages. Thus, to assess whether variation in the time available for subspecies diversification is likely to affect our results, we used a general linear mixed model to test whether subspecies richness is related to species age (i.e. time since cladogenesis) in a sample of Amazonian sister species (Table S5 and S6).

Two other factors commonly influencing patterns of diversification are range size and body mass (Phillimore *et al.* 2007). We controlled for the potential effects of these variables by including them as covariates in species- and genus-level models (data averaged across species in the latter). Prior to all analyses, species and subspecies richness, range size and body mass were log-transformed; and proportions of specialists within a particular ecological category were arcsine transformed. As minimum adequate models can inflate Type I error rates, we report the results of full models, and assess the relative importance of predictors using the change in the deviance information criterion (DIC) between the full model and the model excluding that predictor (Hadfield 2010). Lower values of the DIC indicate higher model support; difference in DIC > 2 indicated a significant effect of the predictor.

Statistical tests were implemented in R. For full details of our phylogenetic framework and modelling approach, see Appendix S1.

RESULTS

Temporal framework

Estimated time since cladogenesis was significantly longer for species (mean ± SE: 3.42 ± 0.4 Ma; $N = 46$ pairs) than for subspecies (0.95 ± 0.18 Ma; $N = 26$ pairs; Table S7, Figure S1), confirming that subspecies are relatively young taxa. (see Appendix S1). Note that these analyses also underestimate the average age of all subspecies and species because they include only sister taxa, which represent the youngest taxa in their respective clades. Thus, even the youngest subspecies generally represent significant genetic divergence, supporting our use of subspecies richness as an index of intra-specific diversification. Our findings also indicate that many Amazonian species, and most subspecies, have diverged since the Amazonian river system became established ~7 Ma (Hoorn *et al.* 2010; Ribas *et al.* 2011).

We found no effect of time since cladogenesis on subspecies richness ($P = 0.53$; Table S8), suggesting that the age of species does not effect the likelihood of subspeciation. Similarly, we found no relationship between clade age (i.e. root age of genus, $N = 283$) and species richness ($r = 0.092$, $P = 0.12$), or mean subspecies richness within genera ($r = -0.008$, $P = 0.89$). This is consistent with a global analysis that found little relationship between species age and subspecies richness in birds (Phillimore 2010). Thus, excluding species and clade age from our main models is unlikely to affect our results. We also note that the lack of relationship between diversity and clade age means that the analyses reported in the following sections are in effect testing for variation in clade carrying capacity (K) rather than clade diversification rate (R) (Rabosky 2009).

Multi-predictor models of diversification

Range size was the most important predictor of species and subspecies richness in all models (Tables 1 and 2), being both highly significant and having the greatest effect on DIC when it was removed. Body mass was the next most important predictor of subspecies richness, but had no significant effect on species richness. Controlling for these effects we found some evidence that ecological specialisms were associated with higher taxonomic diversity. Specifically, in the species-level model (Table 1), we found that subspecies richness tended to be higher in specialists than generalists for three ecological
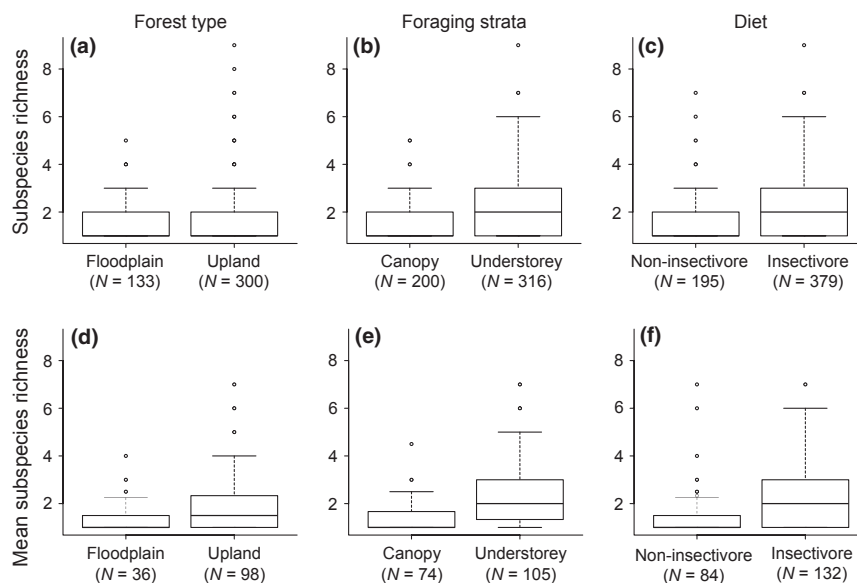

Figure 2 The effect of alternative traits on recent diversification in Amazonian birds. High-dispersal niches (floodplain, canopy, non-insectivory) resulted in significantly lower subspecies richness than low-dispersal niches (upland, understorey, insectivory) at the level of species (a–c) and genus (d–f). Median subspecies richness appears similar across forest types (a), but the difference between means was significant in models of log(subspecies richness). Plots are Tukey box-plots; whiskers show lowest and highest datapoints within 1.5x interquartile range; sample sizes are numbers of genera.

Table 1 Full multi-predictor model investigating the effect of ecological speciali-sation on subspecies richness in Amazonian bird species ($N = 739$)

Main effects	Estimate	P	Δ_{DIC}
Habitat specialism	0.063 (−0.018 to 0.138)	0.118	0.24
Forest-type specialism	0.000 (−0.076 to 0.082)	0.984	−1.85
Strata specialism	0.089 (−0.001 to 0.178)	0.052	0.83
Diet specialism	0.099 (−0.026 to 0.205)	0.096	1.67
Territoriality	0.108 (0.001 to 0.215)	0.055	−1.40
Range size	0.208 (0.174 to 0.242)	< 0.0001	143.73
Body mass	−0.084 (−0.123 to −0.043)	< 0.0001	6.64
Random effects	Variance estimate		
Family	0.027 (0.004 to 0.056)		
Family [genus]	0.017 (0.000 to 0.038)		
Residual variance	0.227 (0.199 to 0.256)		

DIC = 1059.593. Model examines the effect of ecological specialisation on sub-species richness, controlling for range size (log-transformed) and body mass (log-transformed). Values refer to final output from a Bayesian mixed model, with family [genus] as a random effect. Estimates are shown with lower-upper 95% credible intervals. Δ_{DIC} is the change in DIC when the term is removed from the full model.

traits (strata, diet and territoriality). In the genus-level models (Table 2; Figure S3), mean species richness increased significantly with the proportion of territorial species, while mean subspecies richness increased significantly with the proportion of both strata and habitat specialists. Thus, we found a positive, albeit weak, effect on diversification when we pooled all specialisms together regardless of their predicted impact on dispersal.

Comparison between alternative specialisms

In the second set of analyses, phylogenetically controlled compari-sons amongst species and genera revealed that the impacts of spe-cialisms on mean species and subspecies richness is governed by their predicted association with dispersal (Fig. 2, Tables S9 and S10). In each case, specialisms thought to reduce dispersal were associated with higher species or subspecies richness than special-isms thought to increase dispersal. In species-level analyses (Fig. 2a
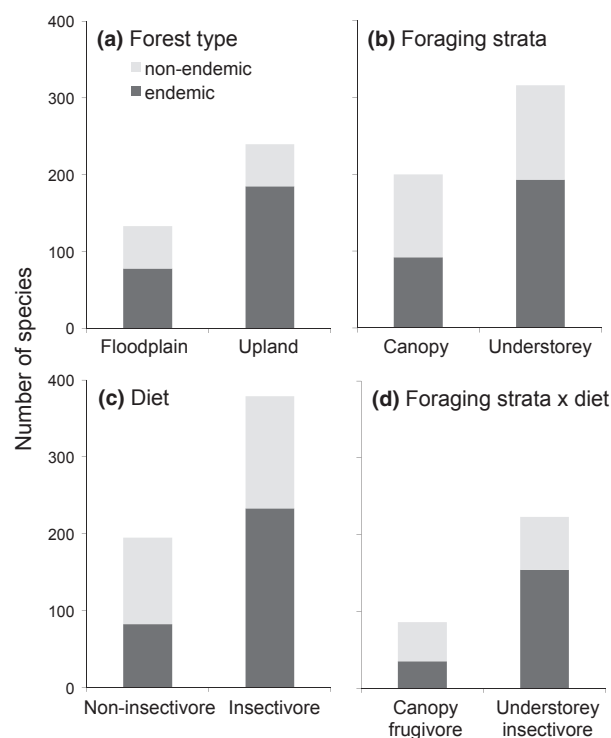

Figure 3 Species richness in Amazonian birds partitioned by alternative traits. High-dispersal niches (floodplain, canopy, non-insectivory) contributed lower numbers of species than low-dispersal niches (upland, understorey, insectivory; a –c); this difference was accentuated when specialisms were combined, for example, canopy frugivores versus understorey insectivores (d). Low-dispersal niches contributed a disproportionately large number of species endemic to Amazonia, particularly when niches were combined (d).

–c; Table S9), we found that subspecies richness was significantly higher in species classified as upland rather than floodplain special-ists [BPMM: parameter estimate (β) = 0.152, credible interval (CI) = 0.036 to 0.266; $P = 0.012$], understorey rather than canopy specialists (β = 0.326, CI = 0.206 to 0.445, $P < 0.0001$), and insecti-vore rather than non-insectivore specialists (β = 0.253, CI = 0.100

Table 2 Full multi-predictor model investigating the effect of ecological specialisation on species and subspecies richness in Amazonian bird genera ($N = 283$)

Main effects	Species			Subspecies		
	Estimate	P	Δ_{DIC}	Estimate	P	Δ_{DIC}
Habitat specialism	−0.205 (−0.345 to −0.070)	0.003	6.59	0.088 (0.004 to 0.175)	0.05	2.41
Forest-type specialism	−0.100 (−0.227 to 0.021)	0.121	0.51	−0.052 (−0.130 to 0.026)	0.195	−1.74
Strata specialism	0.070 (−0.050 to 0.184)	0.252	−0.74	0.137 (0.061 to 0.217)	0.0004	13.64
Diet specialism	−0.029 (−0.157 to 0.102)	0.679	−1.69	0.068 (−0.031 to 0.159)	0.166	−1.10
Territoriality	0.130 (0.009 to 0.238)	0.034	1.74	0.061 (−0.027 to 0.152)	0.179	−5.57
Range size	−0.239 (−0.345 to −0.124)	< 0.0001	14.53	0.217 (0.146 to 0.292)	< 0.0001	50.48
Body mass	−0.017 (−0.079 to 0.047)	0.619	−1.38	−0.099 (−0.158 to −0.043)	0.003	−3.25
Random effects	Variance estimate			Variance estimate		
Phylogenetic	0.023 (0.000 to 0.086)			0.140 (0.035–0.255)		
Residual	0.447 (0.369 to 0.523)			0.138 (0.093–0.182)		

Species DIC = 590.269; subspecies DIC = 314.930. Model examines the effect on species and subspecies richness of the proportion of habitat specialists, forest type specialists, strata specialists, diet specialists, and territorial species within genera, controlling for range size and body mass (averaged across species in the genus and log-transformed). Values refer to final output from Bayesian phylogenetic mixed models. Estimates are shown with lower-upper 95% credible intervals. Δ_{DIC} is the change in DIC when the term is removed from the full model.

to 0.384, $P < 0.0001$). In the genus-level analyses (Fig. 2d–f; Table S10), specialisms linked to reduced dispersal were also strongly positively associated with subspecies richness (upland specialism: $\beta = 0.273$, CI = -0.070 to 0.459, $P = 0.007$; understorey specialism: $\beta = 0.437$, CI = 0.280 to 0.601, $P = 0.0001$; insectivore specialism: $\beta = 0.359$, CI = 0.144 to 0.568, $P = 0.001$). When equivalent comparisons were made for species richness, we found that genera dominated by upland specialists had significantly higher diversity than those dominated by floodplain specialists ($\beta = 0.323$, CI = 0.057 to 0.583, $P = 0.016$). However, no differences in species richness were found between understorey and canopy, or insectivore and non-insectivore specialisms (Table S10).

Linking ecological specialisation with Amazonian diversity

Focusing broadly on the Amazonian avifauna, we found that species richness was unevenly partitioned between niches: low-dispersal niches always made a greater contribution than high-dispersal niches to species richness (Fig. 3). Moreover, a greater proportion of species with low-dispersal niches were endemic to Amazonia, a pattern that was strongly significant for upland vs. floodplain specialists ($\chi^2 = 11.3$, $P = 0.0008$), understorey vs. canopy specialists ($\chi^2 = 14.0$, $P = 0.0002$), and insectivore vs. non-insectivore specialists ($\chi^2 = 19.6$, $P < 0.0001$). The most pronounced patterns were found when comparing species with multiple specialisms – for example, understorey insectivores were represented by more endemic species than canopy frugivores ($\chi^2 = 21.0$, $P < 0.0001$; Fig. 3) – suggesting that greater within-region diversification has occurred in lineages with combinations of specialist traits.

Latitudinal patterns

The number of forest bird species in continental North America (193) is far lower than in Amazonia (739), despite the fact that North America covers a larger geographical area and latitudal range (~30°N–80°N) than Amazonia (~5°N–10°S). These avifaunas also
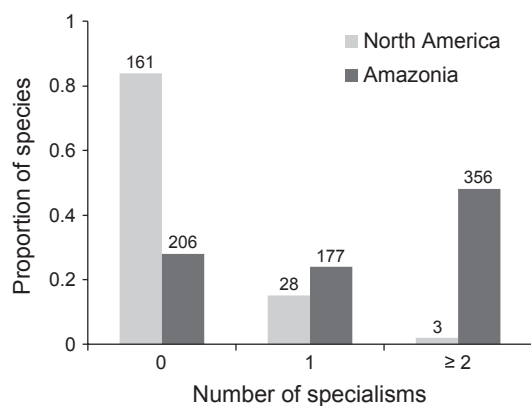

Figure 4 The proportion of forest bird species allocated to ecological specialisms in Amazonia ($N = 739$ species) and continental North America (United States and Canada; $N = 193$ species). Samples were restricted to breeding species; long-distance migrants were treated as non-specialists as they were considered unlikely to be influenced by dispersal constraints. Full list of species and allocation to ecological categories given in Table S2 and S3. Bars show comparisons between proportions of species with 0, 1, and at least 2 specialised ecological traits. The scale of difference is more striking when measured in terms of species (totals given above bars).

differ dramatically in the proportion of species associated with low-dispersal specialisms (Fig. 4). Specifically, non-migratory understorey specialists accounted for 316 Amazonian species (43%), but only nine North American species (5%); non-migratory specialist insectivores accounted for 379 Amazonian species (51%), but only 12 North American species (6%); and year-round territoriality accounted for 316 Amazonian species (43%), but only 14 North American species (7%). These patterns reveal that Amazonia supports a larger proportion of species with low-dispersal niches in terms of foraging strata ($\chi^2 = 122.9$, $P < 0.0001$), diet ($\chi^2 = 143.7$, $P < 0.0001$), and territoriality ($\chi^2 = 109.5$, $P < 0.0001$). The disparity was most extreme for species assigned to any two specialist categories simultaneously: this type of specialist was common in the tropical avifauna, but rare in the temperate zone ($\chi^2 = 187.1$, $P < 0.0001$).

DISCUSSION

We have shown that ecological specialisation drives diversification in Amazonian birds, particularly when specialisms are associated with reduced likelihood of dispersal. When all specialisms were pooled together, the link with diversification was weak, and only significant in the case of strata specialism and year-round territoriality. In contrast, the relationship between low-dispersal niches and higher diversity was strong, presumably because dispersal constraints promote allopatric divergence by limiting gene flow. Our results therefore provide partial support for the dispersal-specialisation trade-off hypothesis set out by Jocque *et al.* (2010), but also highlight the idiosyncratic ways in which ecological specialisation interacts with dispersal to influence patterns of diversification.

Focusing on subspecies richness as an index of intra-specific diversification, foraging strata emerged as a key predictor in all analyses. This is consistent with the finding that understorey specialism predicts the degree of genetic divergence across biogeographic barriers in Neotropical birds (Burney & Brumfield 2009). The importance of strata specialism is almost certainly linked to the fact that many bird species restricted to rainforest understorey are averse to crossing open spaces (Stratford & Robinson 2005), including narrow stretches of water (Moore *et al.* 2008). Thus, any gaps in forested habitat, such as major Amazonian rivers, present much stronger barriers to gene flow for understorey species. The same mechanism may also explain the higher subspecies richness associated with year-round territoriality and insectivory, as these traits are again associated with reduced gap-crossing ability (Levey & Stiles 1992; Moore *et al.* 2008).

The strength of biogeographical barriers may be influenced not only by dispersal ability, but by dispersal likelihood. Habitat specialists may cross barriers less often simply because the gaps between suitable habitats are wider, potentially influencing movement patterns. Similarly, our finding that upland specialism is positively associated with subspecies richness is probably related to the greater effective width of floodplains as dispersal barriers for upland species (Hayes & Sewlal 2004). Thus, intrinsic traits – such as specialism to particular habitats and forest-types – may limit dispersal across extrinsic barriers via mechanisms that are not explained by dispersal ability alone.

A similar combination of factors acts in reverse to increase dispersal across barriers. Frugivory and canopy specialism are associated with high dispersal ability, often permitting active movement across broad gaps in habitat (Levey & Stiles 1992; Hayes & Sewlal 2004; Burney & Brumfield 2009). In addition, restriction to floodplains is likely to promote dispersal across rivers even for non-vagile species, as channel

migration and oxbow lake formation can transfer individuals passively from bank to bank (Haffer 1997). Our finding that these ecological traits are associated with reduced subspecies richness is consistent with an increased potential for gene flow between populations. Conversely, the same pattern conflicts with the central prediction of the biotic interactions hypothesis (Dobzhansky 1950; Schemske *et al.* 2009) that diversification is promoted by specialised associations – which in our dataset are strongest between frugivores or nectarivores and their food plants.

The link between ecological specialisation and subspecies richness rather than species richness implies that dispersal-related mechanisms are important in the early stages of speciation but contribute relatively little to diversity at the species level, perhaps because they generate geographic variation rather than reproductive isolation. However, this is not necessarily the case, as weaker patterns may simply reflect the limitations of species-level models (see Appendix S1). Indeed, when we conducted analyses on the relative contributions of different niches to the Amazonian avifauna, we found that low-dispersal niches not only account for more species richness, but also a far greater proportion of endemic species (Fig. 3). These patterns suggest that Amazonian speciation has been predominantly driven by mechanisms related to low-dispersal specialisms.

Dispersal-mediated speciation could have far-reaching implications for the LDG if the evolution of low-dispersal niches is skewed towards the tropics, which seems likely to be the case. Greater numbers of understorey specialists, for example, may arise as a byproduct of the high structural complexity of tropical forests (MacArthur 1964), while other non-migratory specialisms involving year-round territoriality and insectivory may proliferate in stable tropical climates (Tobias *et al.* 2011). In support of this view, a basic survey reveals that at least one of these key specialisms is found in 532 species in Amazonia (72%), compared with only 31 forest bird species in North America (16%). The disparity was even more pronounced for combined specialists – that is, lineages with at least two specialist traits – as these were extremely rare outside the tropics (Fig. 4).

These findings can be interpreted in different ways. One possibility is that temperate regions have only recently been colonised, in which case non-vagile lineages may be slowest to arrive. However, this seems unlikely in much of the southern United States, as this region lies beyond the southernmost extent of ice during glacial maxima. Alternatively, specialists may be less likely to prosper in the temperate zone because climatic conditions are unsuitable – perhaps the most obvious cases are specialist insectivores, few of which can survive year-round in temperate forests where their dietary niche is seasonal (Belmaker *et al.* 2011). Both these mechanisms may contribute to the patterns observed, but we suspect that climatic factors are prominent. Either way, the existence of latitudinal gradients in low-dispersal specialisms suggests that lineages susceptible to allopatric speciation are far more numerous in equatorial systems, and that lineage-splitting events are thus rarer in the temperate zone.

A lack of association between diversification and ecological specialisation would support purely abiotic explanations for Amazonian diversity, including those related to climate (Hawkins *et al.* 2003), geological history (Hoorn *et al.* 2010) and time (Wiens *et al.* 2011). Instead, our analyses revealed the converse, highlighting the role of deterministic biotic processes mediated by inherent ecological traits. In addition, our results appear to counter those of global scale analyses showing that diversification rates are positively associated with high annual dispersal and dietary generalism in birds (Phillimore *et al.* 2006). We suggest that these factors are relevant mainly to insular or temperate systems where long-distance (peripatric) speciation is a major source of diversity, and that ecological specialisation and associated dispersal constraints are key factors in the continental tropics, where most of the world's biodiversity is found.

The importance of low rates of dispersal in reducing the homogenising effect of gene flow and thus promoting divergence and speciation has long been recognised (Wright 1940; Ikeda *et al.* 2012). Indeed, there is growing evidence that ecological dispersal constraints act as drivers of diversification in continental radiations of animals, including birds (Burney & Brumfield 2009; Claramunt *et al.* 2012). However, this study is the first to demonstrate that ecological specialisation predicts the scale of diversification, with an impact heavily weighted towards tropical systems. It therefore suggests that niche-related dispersal constraints are a key evolutionary mechanism behind the LDG, potentially explaining the overall spatial pattern of increasing biodiversity towards the tropics, in parallel with increasing specialisation (Belmaker *et al.* 2011).

Taken together, our results provide evidence that ecological specialisation shapes broad-scale patterns of biodiversity, and that it does so because dispersal limitation promotes allopatric speciation. They therefore shift the focus away from the traditional concept that narrower tropical niches permit diversity to build up by species packing in sympatry (MacArthur 1964; Vázquez & Stevens 2004) and instead highlight their role in reducing gene flow between populations. We propose that at any given time a vast number of different lineages and sublineages are undergoing slow allopatric divergence mediated by dispersal constraints in the continental tropics, greatly outweighing the equivalent number in the temperate zone, and adding an extra dimension to tropical diversification that is not explained by purely abiotic factors.

AUTHORSHIP

CS, NS and JAT developed conceptual framework and devised analytical approach, CS and JAT collected data, CC, NS and CS performed analyses, CS and JAT wrote the manuscript.

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