



Body size and latitudinal gradients in regional diversity of New World birds

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ABSTRACT

Are latitudinal gradients in regional diversity random or biased with respect to body size? Using data for the New World avifauna, I show that the slope of the increase in regional species richness from the Arctic to the equator is not independent of body size. The increase is steepest among small and medium-sized species, and shallowest among the largest species. This is reflected in latitudinal variation in the shape of frequency distributions of body sizes in regional subsets of the New World avifauna. Because species are added disproportion-

ately in small and medium size classes towards low latitudes, distributions become less widely spread along the body size axis than expected from the number of species. These patterns suggest an interaction between the effects of latitude and body size on species richness, implying that mechanisms which vary with both latitude and body size may be important determinants of high tropical diversity in New World birds.

Key words Beta-diversity, birds, body size distributions, latitudinal gradients, macroecology, New World avifauna, species richness.

INTRODUCTION

Most major taxonomic groups show an increase in species richness from high latitudes towards the equator. Many hypotheses have been offered to explain this well-known pattern (Rohde, 1992, 1999; Rosenzweig, 1995; Gaston, 2000), but an explanation which is widely accepted by biologists remains elusive. One approach is to ask whether the addition of species towards the equator occurs randomly, or if there is a disproportionate addition of species with certain characteristics. For animals, an obvious trait to examine in this respect is body size. Body size constrains many life history and ecological traits of a species (Peters, 1983), and appears to have a strong influence on the diversification and structure of animal assemblages at macroecological scales (Brown & Maurer, 1989; Brown *et al.*, 1993; Blackburn & Gaston, 1994). Furthermore, in some groups mean body size appears to decrease towards the equator, both within and between species (Cushman *et al.*, 1993; Blackburn & Gaston, 1996a; Brown & Lomolino, 1998), implying latitudinal diversity gradients which are non-random with respect to body size (Blackburn & Gaston, 1996b). Because species richness is also non-random with respect to body size (Blackburn & Gaston, 1994; Brown, 1995), examining the effect of body size on latitudinal diversity gradients may shed light on processes underlying high species richness in the tropics.

Whether or not latitudinal diversity gradients are biased by body size, and what the nature of this bias is, could be

revealed by examining how the shapes of body size frequency distributions change to accommodate more species, as we move from high to low latitudes. If species are added randomly across the body size spectrum, we would expect the body size distributions for tropical assemblages to be very similar in shape to those for temperate assemblages, once the difference in the number of species is allowed for. On the other hand, species might be added non-randomly, with a disproportionate increase on certain parts of the body size axis. For example, if mean body sizes are lower in the tropics, this might be due to: (1) a reduced lower bound of the body size axis, (2) a reduced upper bound of the body size axis, (3) an increase in species number around the modal size, given that body size distributions of large-scale assemblages are typically unimodal and log-right skewed (Blackburn & Gaston, 1994), or (4) an increase in species number at the smallest sizes.

In this study, patterns of body size and species richness for New World land bird assemblages are analysed among nine regions along a gradient from the arctic to the equator. I examine, first, whether latitudinal gradients in regional diversity are non-random with respect to body size, and secondly, whether any non-randomness is reflected in latitudinal variation in the shape of body size distributions. Regional, rather than local, patterns, are focused upon as it has become widely accepted in recent years that large-scale patterns such as latitudinal diversity gradients are determined predominantly by processes operating at regional scales (Ricklefs & Schluter,

1993). The idiosyncracies of local communities are transcended at regional scales: assemblages are more likely to be structured by the long-term dynamics of speciation, extinction and colonization than by local ecological processes such as competition (Brown & Maurer, 1989; Brown, 1995; Maurer, 1999). For these reasons, patterns observed at regional scales are more likely to reflect the processes underlying latitudinal diversity gradients than local-scale patterns.

METHODS

The bird data

All analyses were based on bird assemblages within nine regions of the New World, spanning a latitudinal gradient from 61°N to 1°N (Table 1). The regions are defined for convenience by political boundaries: part of the US state of Alaska (the south-east corner bounded by longitudes 141°E and 148°E, latitude 64°N and the south coast); part of the Canadian province of Manitoba (the southern portion that lies within the area covered by the North American Breeding Bird Survey); the entire US states of Wisconsin, Illinois and Mississippi; Guatemala plus Belize; Nicaragua; Surinam; and the Brazilian state of Amapá. These regions are of roughly equal size; this is important because the shape of body size distributions changes with spatial scale (Brown & Nicoletto, 1991). For each region, a list of breeding land birds was compiled from the North American Breeding Bird Survey (Sauer *et al.*, 1999) or published regional or national bird checklists and atlases (the dataset is available on request). Non-breeding seasonal migrants or species primarily aquatic in habitat preference were not included. All species were converted to the nomenclature of Sibley & Monroe (1990) to eliminate synonymy. Body sizes (mass in grams) for approximately 79% of species were obtained from published sources, primarily Dunning (1993). For species of

unknown body size that were part of a relatively large genus (> 10 species), size was estimated from length–mass regressions among species from the same genus. For species from smaller genera, I did not attempt to estimate size.

Body size and latitudinal diversity gradients

To examine latitudinal diversity gradients for birds of different body sizes, body sizes were divided into five logarithmic size groups and the number of species calculated in each. I then tested for heterogeneity of slopes among the different size groups by including the interaction between size group and latitude as a term in a general linear model, with species richness as the response variable. Latitude is the latitudinal midpoint of each of the nine regions. A significant effect of the interaction term on species richness indicates that the slope of the species richness — latitude relationship does vary with body size. To account for the slight variation in the size of the nine regions, geographical area was also included as a covariate in the model. The same method was then used to carry out pairwise comparisons of slopes for all body size groups.

Shape of body size frequency distributions

For the bird assemblage in each of the nine regions, the shape of the frequency distribution of \log_{10} -transformed body sizes was described by the following statistics: mean, standard deviation, skewness, 10th percentile, 90th percentile and range. 10th and 90th percentiles were used to describe the lower and upper body size bounds because absolute minimum and maximum are determined by single species, so a single extreme value could bias the statistic for an entire distribution. Range is the difference between the 10th and 90th percentiles. These statistics should reflect the way in which species are added to an assemblage. For example, if tropical assemblages simply represent larger random samples from the same species pool, we should see an increase towards the equator in the body size range, a lower 10th percentile and higher 90th percentile, and no change in standard deviation, skewness or mean body size.

In comparing body size distributions among the nine regions, it was important to factor out the effects of species richness variation, because a richer assemblage is expected to cover a wider range of body sizes, and richness may thus influence several of the statistical parameters describing the shape of the distributions. With this in mind, the data were analysed in two ways. First, general linear models were used to test for effects of latitude on each body size distribution statistic, with land area and species richness entered as covariates in the model ahead of latitude. Because two of the predictor variables in this model are intercorrelated (richness and latitude), the richness–latitude interaction was also included as a term in the model. A non-significant effect of this interaction term

Table 1 The nine subregions of the New World used in this study, showing the latitudinal midpoint in degrees north of the equator, land area (approximate land areas for south-east Alaska and southern Manitoba) and species richness of breeding land birds

Region	Latitudinal midpoint (degrees north)	Land area (km ²)	Species richness
South-east Alaska	61	148 000	90
Southern Manitoba	50	162 000	157
Wisconsin	45	140 965	160
Illinois	40	144 120	130
Mississippi	33	122 335	106
Guatemala + Belize	16	131 855	439
Nicaragua	13	148 000	415
Surinam	4	163 820	519
Amapá	1	140 275	478

indicates that any effect of latitude on the response variable is independent of any variation in species richness.

Secondly, a null-model approach was used, comparing the statistics for each region with those of the same number of species drawn randomly (1000 times with replacement) from a larger species pool. The species pool was defined as the set of all species occurring within any of the nine regions included in this study. For each statistic, two-tailed probabilities were calculated as the proportion of values from the null distribution which were more extreme than the observed value, multiplied by two. These probabilities give the likelihood that a statistic differs from what is expected if the regional assemblages are simply different-sized random subsets of the New World avifauna. Latitudinal variation in these probabilities indicates changes in the shape of body size distributions with latitude, which are independent of species richness.

RESULTS

Body size and latitudinal diversity gradients

The general linear model analysis indicates that bird species richness across the nine regions increases from high to low latitudes at different rates, depending on body size (Table 2). This is shown by the significant effect on species richness of the interaction between body size group and latitude, once the effect of land area has been accounted for. From Fig. 1, it is apparent that the slope of the increase is steepest in the smallest size group, slightly less steep in intermediate size groups and shallowest in the largest size group, suggesting that species of small and medium sizes are added disproportionately as we move from high latitudes towards the equator. Pairwise comparisons of slopes between the five size groups indicate that the slope for the largest size group is significantly shallower than those for all other size groups ($P < 0.01$), the smallest size group has a steeper slope than the next-largest group ($P = 0.04$), and all other comparisons are non-significant ($P > 0.05$). However, it is also evident from Fig. 1 that species richness does not increase continuously with

Table 2 Results of general linear model analysis (based on Type 1 sums of squares) with \log_{10} species richness as the response and land area, latitude, body size group and the latitude \times body size interaction as predictors. The significance of the interaction term indicates a strong body size effect on the slope of the species richness–latitude relationship. $N = 9$ for all tests

	d.f.	<i>F</i>	<i>P</i>
Land area	1	6.5	0.02
Latitude	1	138.33	0.0001
Body size group	4	96.04	0.0001
Latitude \times body size group	4	5.43	0.002

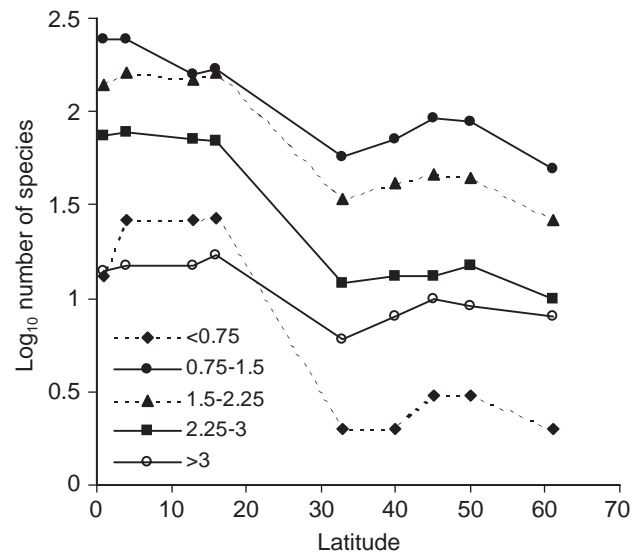


Fig. 1 Latitudinal gradients in species richness of breeding land birds (\log_{10} number of species) among nine New World regions, in five body size groups (\log_{10} g).

decreasing latitude. Rather, the increase appears to be step-wise, the greatest difference in richness being between the Nearctic regions (61° – 33°) and the Neotropical regions (16° – 1°), with relatively minor variation in richness within these two regions. Hence, the effect of body size on the slope of these gradients applies mainly to the difference in species richness between the Nearctic and the Neotropics.

Shape of body size frequency distributions

Figure 2 shows body size frequency distributions for the nine regional bird assemblages. Two methods were used for analysing variation with latitude in the shape of these distributions, while controlling for variation in species richness. Table 3 shows results of general linear models with each statistic describing the shape of distributions as the response variables, and land area, species richness, latitude and the species richness–latitude interaction as predictors. These results indicate that once land area and species richness are controlled for, there are significant positive effects of latitude on the standard deviation, 90th percentile and range of the body size distributions. Non-significant interaction terms indicate that these latitudinal effects are independent of any variation in species richness. There are no significant effects of latitude on the mean, skewness or 10th percentile of the distributions. These results indicate that towards the equator, species become less widely distributed along the body size axis than would be predicted from the increase in species numbers. The significant variation in the upper bound (90th percentile) but not in the lower bound (10th percentile) indicates that the position

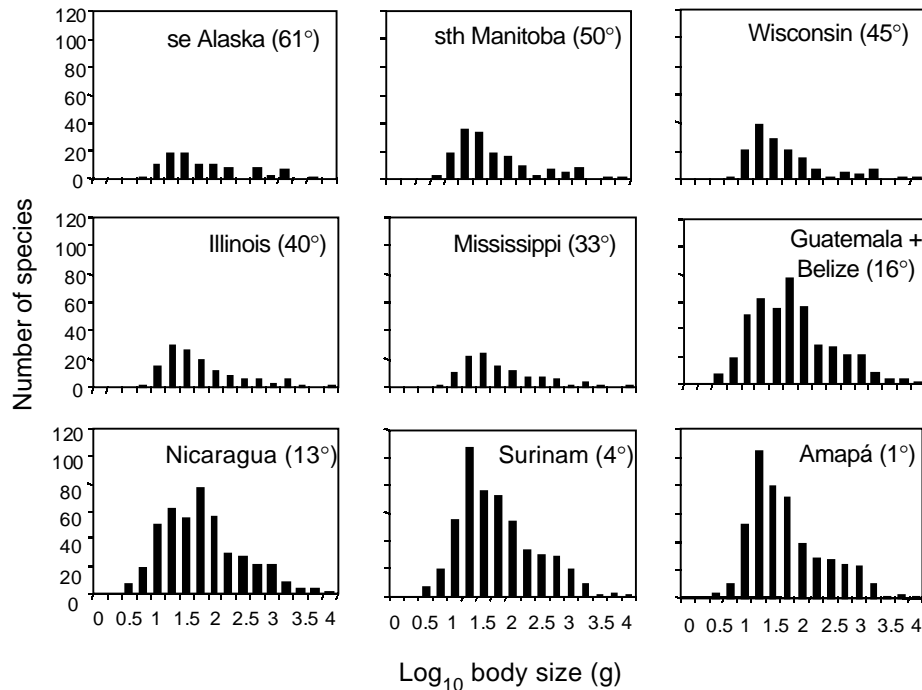


Fig. 2 Frequency distributions of body mass (\log_{10} g) for breeding land birds, in nine New World regions of approximately equal land area. Latitudinal midpoints in degrees north are shown.

Table 3 Results of general linear model analyses (based on Type 1 sums of squares) with six statistics describing the shape of body size distributions as response variables, and land area, species richness, latitude and the species richness–latitude interaction as predictors. Values shown are *P*-values, with direction of slope indicated in brackets for main effects. The non-significant interactions indicate that the effects of latitude are independent of any variation in species richness

Statistic	Area	Species richness	Latitude	Species richness \times latitude
Mean	0.75 (–)	0.69 (+)	0.48 (+)	0.96
Standard deviation	0.33 (–)	0.99 (+)	0.02 (+)	0.86
Skewness	0.83 (+)	0.04 (–)	0.49 (–)	0.90
10th percentile	0.56 (+)	0.005 (–)	0.15 (–)	0.06
90th percentile	0.19 (–)	0.09 (+)	0.01 (+)	0.81
Range	0.25 (–)	0.30 (+)	0.02 (+)	0.33

of the upper bound remains relatively constant in absolute terms as species numbers increase towards the equator, but the lower bound stretches to accommodate the extra species.

The results of the null model tests do not indicate any continuous latitudinal trends for the statistics describing body size distributions (Fig. 3). Overall, the null model tests indicate that the body size distributions of the nine regions are mostly not significantly different from random subsets of the broader species pool. Exceptions are the two Central American regions, Guatemala + Belize (16°) and Nicaragua (13°), which are significantly different from random for all statistics except 10th percentile. These two regions have a higher mean body size, a greater standard deviation, are less right-skewed, have

a higher upper body size bound and a wider range of body sizes than expected by chance.

DISCUSSION

The results of this study confirm previous demonstrations of strong latitudinal gradients in regional species richness of New World birds (Cook, 1969; MacArthur, 1969; Blackburn & Gaston, 1996b). The highly stepwise pattern of increase in species richness towards the equator in my study is partly a function of the particular regions chosen: the area around Manitoba and Wisconsin seems to have relatively high species richness for its latitude, while the area around Mississippi has

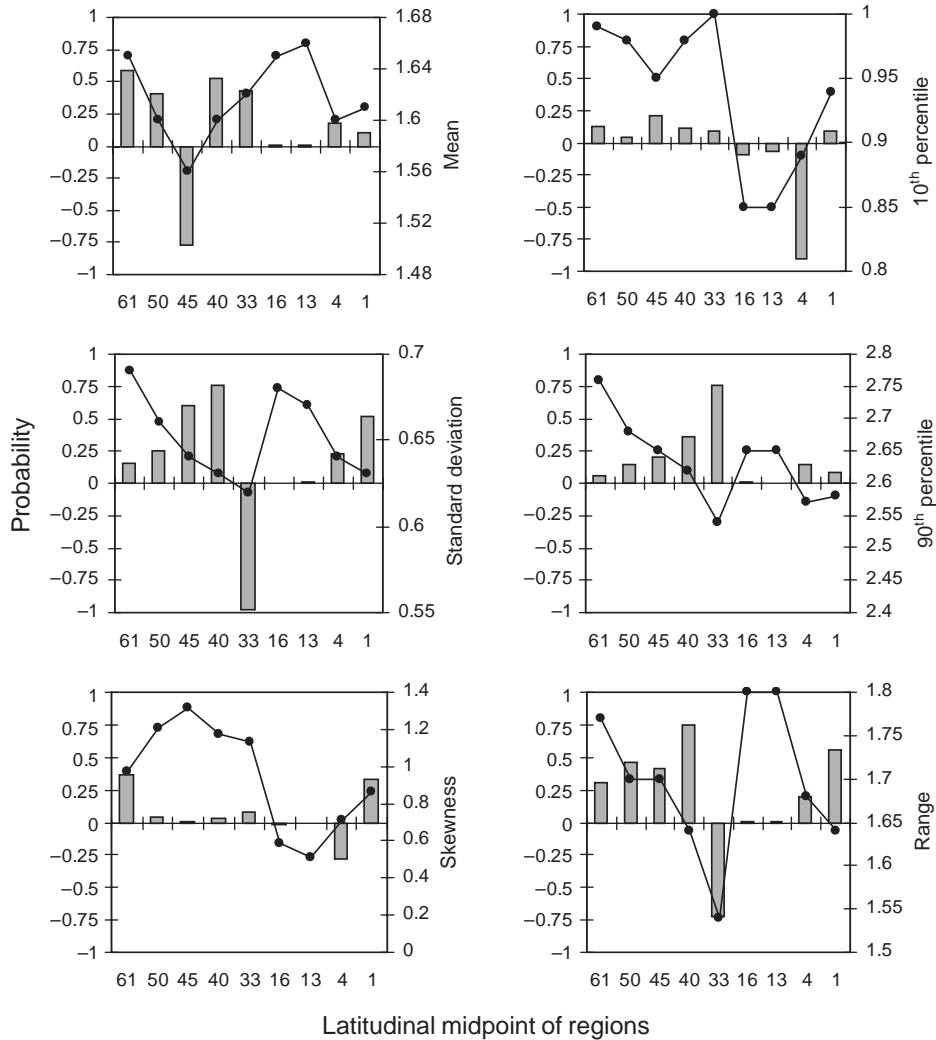


Fig. 3 Results of null-model tests for non-randomness in six statistics describing body size frequency distributions. Each graph shows the value of a statistic (dots connected by lines, scales on the right of each graph) in nine New World regions. Latitudinal midpoints of the regions are shown on the x -axis, and distributed evenly along the axis for clarity. Bars show the probability (scales on the left of each graph) that each value of the statistic is significantly different from that obtained by randomly drawing the same number of species from a broader species pool. Probabilities are positive or negative depending on whether the observed value fell within the upper or lower tail, respectively, of the null distribution.

relatively low species richness (Cook, 1969; MacArthur, 1969; Blackburn & Gaston, 1996b). Cook's (1969) north-south transect through the centre of North America shows a similar stepwise increase in species richness to that shown here, whilst his transect through the western part of the continent is somewhat smoother. Nevertheless, the overall pattern of species richness variation in North America appears to be a relatively shallow increase from the Arctic to approximately 30° north, then a very steep increase to the tropics (Cook, 1969; Blackburn & Gaston, 1996b). Therefore, the latitudinal diversity gradient across these nine regions is probably representative of the pattern for the northern half of the New

World overall. This study furthers the analyses by the above authors by demonstrating that the increase in species richness towards low latitudes occurs mostly among species of small to medium body size, and that the shape of body size distributions vary accordingly.

One common concern with analyses of large-scale species assemblages is the possibility of results being confounded by phylogenetic relationships among species. Much of the land bird diversity of the New World can be attributed to the four largest families: Fringillidae (660 species), Tyrannidae (433), Thamnophilidae (356) and Trochilidae (240). Latitudinal variation in the representation of any of these families could

Table 4 Tests for the influence of the four largest New World bird families on the results of the GLM analyses presented in Table 3. The table shows the significance of the effect of latitude and the species richness–latitude interaction (with area and species richness controlled for) on standard deviation, range and 90th percentiles of body size distributions, with each of the four families removed from the analysis. The results indicate that the significant patterns for birds overall shown in Table 3 are robust to the removal of these families

Family removed	Standard deviation		Range		90th percentile	
	Latitude	Species richness × latitude	Latitude	Species richness × latitude	Latitude	Species richness × latitude
Fringillidae	0.003	0.06	0.02	0.11	0.05	0.53
Thamnophilidae	0.03	0.17	0.03	0.38	0.07	0.13
Trochilidae	0.008	0.29	0.02	0.80	0.04	0.79
Tyrannidae	0.01	0.33	0.01	0.74	0.09	0.33

potentially cause the patterns observed in the analysis of the entire assemblage. To test this the general linear model analyses of body size distribution statistics were repeated against latitude four times, with one of these families removed each time. All the significant patterns remain qualitatively the same, although in some cases the probabilities become marginally non-significant (Table 4). While this is only a rough way of controlling for phylogenetic bias, it does suggest that latitudinal variation in body size distributions is not simply a result of changing phylogenetic composition at the family level.

The results of the null-model tests raise the possibility that the overall latitudinal effects on body size distributions are strongly influenced by the unusual shapes of the distributions in the two Central American regions (Guatemala + Belize and Nicaragua), rather than resulting from any systematic latitudinal effect. These two regions were largely non-random in their body size distributions while the other regions were, for the most part, not significantly different from random subsets of the broader species pool. From Fig. 1 it is evident that the body size distributions of the two Central American regions differ from the distributions in the South American regions (Surinam and Amapá) in that they lack the distinct peak in richness in the size class with a midpoint of \log_{10} 1.25 g (approximately 17.8 g). This peak can be attributed mostly to the large South American radiation of the family Tyrannidae. With this family removed from the dataset, however, latitudinal effects on body size distributions still hold (Table 4). This suggests that the observed patterns of latitudinal variation in body size distributions are more than the simple consequence of the biogeographic and phylogenetic history of the New World avifauna.

The most likely general explanation for the body size bias in the latitudinal diversity gradient for New World birds is that there is an interaction between variation in species richness with latitude, and variation in species richness with body size. That there is an increase in numbers of bird species of all body sizes from high latitudes towards the equator has been shown here and elsewhere, and is beyond doubt. It is also obvious that numbers of species are distributed heterogene-

ously with respect to body size: for most large assemblages of animals, including birds, smaller body size classes contain the most species, although species numbers usually drop off steeply at the very smallest body sizes (Blackburn & Gaston, 1994; Brown, 1995). If the mechanisms which promote higher overall species richness at low latitudes are the same as those which promote higher species richness at smaller body sizes, then we expect smaller body size groups to show steeper latitudinal diversity gradients. This would suggest that mechanisms which vary with both latitude and body size may be important determinants of high tropical species richness in New World birds. Previously proposed mechanisms which may meet this criterion include the rate of cladogenesis, niche breadth, geographical range size and Beta diversity.

Unfortunately, the evidence with which to assess these mechanisms is limited. There is some evidence that rate of cladogenesis in birds increases towards low latitudes (Cardillo, 1999), but recent phylogenetic studies have failed to find a link between rate of cladogenesis and body size in birds (Nee *et al.*, 1992; Owens *et al.*, 1999). Niche breadth, in terms of habitat and food specificity, has long been suspected to contribute to both latitudinal and body size variation in species numbers (Dobzhansky, 1950; Hutchinson & MacArthur, 1959; Pianka, 1966; MacArthur, 1969), but phylogenetically controlled empirical evidence to support these suspicions is lacking. The decreasing latitudinal extent of geographical ranges towards low latitudes has been suggested to increase regional diversity in the tropics by spillover of species beyond their usual range limits (Stevens, 1989). In New World birds, smaller-bodied species do tend to have smaller geographical ranges, but geographical range sizes reach a minimum not at the equator but at approximately 17° north (Blackburn & Gaston, 1996c). Perhaps the most promising mechanism, based on current data, is the increase in Beta diversity (spatial turnover of species) towards the equator. Although correlated with range size, Beta diversity in New World birds reaches a maximum close to the equator (Blackburn & Gaston, 1996d). If smaller species have smaller geographical ranges and hence higher Beta diversity, this

should result in smaller species having highest rates of increase in Beta diversity from high to low latitudes. Because Beta diversity is a component of regional species richness, this may contribute to the steeper increase in regional species richness seen in small to medium size groups. Clearly, a detailed investigation of mechanistic associations between body size and species richness, and their potential contribution to latitudinal diversity gradients, is needed. More generally, the recent trend towards dissecting latitudinal diversity gradients (Roy *et al.*, 1999), by examining second-order variation in gross patterns of species richness increase towards the equator, should be a useful approach to understanding the causes of high tropical diversity.

ACKNOWLEDGMENTS

Many thanks to Ian Owens, Phillip Cassey and Hugh Possingham for comments. I am supported by a University of Queensland Graduate School Award.

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BIOSKETCH

Marcel Cardillo has research interests in macroecology and the use of phylogenetic comparative methods to investigate patterns and correlates of species diversity and contemporary extinction risk, particularly in bird and mammal faunas.