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Global analysis of bird elevational diversity

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ABSTRACT

Aim Elevational gradients distributed across the globe are a powerful test system for understanding biodiversity. Here I use a comprehensive set of bird elevational gradients to test the main drivers of diversity, including sampling, area, mid-domain effect, temperature, temperature and water availability, and hypotheses of evolutionary history.

Location Seventy-eight elevational gradients of bird diversity from mountains in both hemispheres spanning 24.5° S to 48.2° N, including gradients from various climates, biogeographical regions and habitat types.

Methods Data on bird elevational diversity were taken from the literature. Of the 150 datasets found or compiled, only those with a high, unbiased sampling effort were used in analyses. Datasets sampled all birds, all breeding birds or all forest birds; a few studies detailed seasonal, elevational shifts. Eighteen predictions of diversity theory were tested, including three sets of interactions.

Results Birds display four distinct diversity patterns in nearly equal frequency on mountains: decreasing diversity, low-elevation plateaus, low-elevation plateaus with mid-peaks, and unimodal mid-elevational peaks. Bird elevational diversity strongly supports current climate as the main driver of diversity, particularly combined trends in temperature and water availability. Bird diversity on humid mountains is either decreasing or shows a low-elevation plateau in diversity, while on dry mountains it is unimodal or a broad, low-elevation plateau usually with a mid-elevation maximum. The predictions of sampling, area and mid-domain effect were not consistently supported globally. The only evolutionary hypothesis with preliminary support was niche conservatism.

Main conclusions Both water and temperature variables are needed to comprehensively predict elevational diversity patterns for birds. This result is consistent for breeding and forest birds, for both hemispheres, and for local- or regional-scale montane gradients. More analyses are needed to discern whether the mechanism underlying these relationships is ecological, based on direct physiological limitations or indirect food resource limitations, or historical, based on phylogenetic niche conservatism or other evolutionary trends related to climate. The species–area and mid-domain effects are not supported as primary drivers of elevational diversity in birds.

Keywords

Avian, climate, environmental gradient, evolutionary history, mid-domain effect, mountains, species–area relationship, species richness, temperature, water availability.

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INTRODUCTION

The complexity of bird diversity patterns and their underlying causes was depicted in recent global analyses (Hawkins *et al.*,

2003a, 2007a; Orme *et al.*, 2005; Rahbek *et al.*, 2007). Bird diversity was highest in tropical montane regions, but models of diversity mechanisms consistently underpredicted montane diversity (e.g. Rahbek *et al.*, 2007). One reason for this disjunct is

scale. The strong elevational shifts in climate, habitat and topography occur at scales of 1 to 10 km, whereas the scales of global analyses were orders of magnitude larger (110 km² to 1° × 1° latitude–longitude). Such large scales average much of the important variation in the potential drivers imperative for deciphering the high richness of montane systems (e.g. Ruggiero & Hawkins, 2008). Even the earliest biologists – Aristotle, von Humboldt, Darwin, Wallace – were influenced by dramatic abiotic and biotic changes occurring within short distances on montane gradients when forming their first ideas about life on earth and evolution. Our fundamental understanding of niche concepts (e.g. Grinnell, 1917; Grinnell & Storer, 1924), life zones (e.g. Merriam & Stejneger, 1890), community structure, gradient analysis and beta diversity (e.g. Whittaker, 1952, 1960, 1967) came directly from studies on montane gradients. The examination of diversity gradients on mountains also offers a dynamic and potentially powerful, complementary approach to global-scale studies by utilizing a large number of independent, replicated gradients at a smaller scale (Brown, 2001; Lomolino, 2001; McCain, 2005, 2007a).

Four aspects of mountain systems make them ideally suited for examining biodiversity drivers: globally replicated gradients, spatial scale, power of theoretical tests and variability of the taxonomic signal. Thousands of elevational gradients are distributed across the globe on all continents and on most islands in various latitudes, climates and habitats. The power to differentiate between diversity theories along the terrestrial, latitudinal gradient is hindered because the main diversity theories (climate, area, spatial constraints, history) are correlated and confounded along the two replicate gradients in the eastern and western hemispheres (e.g. Pianka, 1966; Rohde, 1992; Brown & Lomolino, 1998; Willig *et al.*, 2003). With the multitude of elevational gradients distributed across the globe, the power to differentiate between diversity theories increases since each gradient displays a slightly different array of variables (e.g. area, rainfall, evolutionary history), thus allowing tests to distinguish between correlated and confounded variables by seeking globally consistent trends for each factor. Lastly, almost all groups of organisms exhibit one latitudinal pattern in diversity: unimodal with diversity peaking near the equator (e.g. Hillebrand, 2004). Several diversity patterns are exhibited on montane gradients (see Fig. 1; Rahbek, 1995, 2005; McCain, 2005, 2007a): decreasing diversity with increasing elevation, high diversity across a plateau of lower elevations then decreasing monotonically, a unimodal pattern with maximum diversity at intermediate elevations, or in rare instances increasing monotonically. These patterns appear to differ within and among taxonomic groups and climates (McCain, 2005, 2007a). Variability in taxonomic signal, variability in potential drivers on individual gradients, and the array of elevational gradients sampled historically can be used to determine the most influential drivers of diversity in powerful, combined analyses.

Proposed drivers of biodiversity can be grouped into four main categories: current climate, space, evolutionary history and biotic processes (Pianka, 1966; Gaston, 2000; McCain, 2007a). Climatic hypotheses are based on current abiotic conditions,

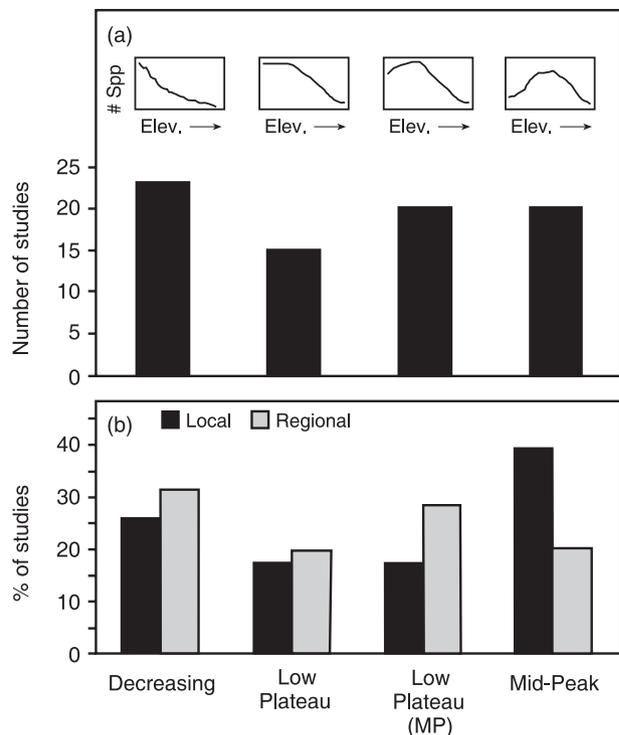


Figure 1 (a) The number of bird studies demonstrating the four elevational richness patterns on the robust, informative montane gradients ($n = 78$): decreasing, low plateau, low plateau with a mid-elevational peak and mid-elevational peaks (see text for definitions). (b) Comparison of the percentage of each bird diversity pattern in the local- and regional-scale studies ($n = 23$ and 55 , respectively); the frequency of each elevational diversity pattern is not significantly different between scales ($X^2 = 3.03$, d.f. = 3 , $P = 0.387$).

such as temperature, rainfall, productivity, humidity and cloud cover. Spatial hypotheses include the classic species–area relationship (SAR; e.g. Terborgh, 1973; Rosenzweig, 1992, 1995) and spatial constraint hypothesis (the mid-domain effect, MDE; e.g. Colwell *et al.*, 2004, 2005). Speciation rates, extinction rates, clade age and phylogenetic niche conservatism are theoretically linked and, in some cases, empirically linked to diversity (e.g. Rohde, 1992; Allen *et al.*, 2002; Stephens & Wiens, 2003; Wiens *et al.*, 2006; Mittelbach *et al.*, 2007). Lastly, various biological processes have been proposed to explain patterns in species richness. These include competition (e.g. Terborgh & Weske, 1975), source–sink dynamics and ecotone effects (e.g. Terborgh, 1985; McCain, 2004), habitat heterogeneity (e.g. MacArthur & MacArthur, 1961) and habitat complexity (e.g. Terborgh, 1977). Tests of the effect of these biotic processes on diversity patterns are minimal due to the difficulty in defining critical characteristics as well as measuring these traits for all species along a large spatial gradient.

Many of proposed drivers of global biodiversity are testable along elevational gradients studied over the last century of research on montane birds around the world (Table 1). Complete multivariate analyses are not yet possible due to data limitations, particularly: (1) lack of global, small-scale (10s to

Table 1 Currently testable hypotheses and predictions for bird diversity on elevational gradients.

Hypothesis:	Theory	Montane testable predictions
Sampling	Diversity is positively related to survey effort	A. Diversity at each 100-m elevational band will be positively correlated to sampling effort in that elevational band B. Local-scale studies (standardized sampling effort per elevation) should show a different frequency of elevational diversity patterns from non-standardized regional studies
Area	Diversity is positively related to land area	A. Diversity at each 100-m elevation band will be positively related to area at that elevation for regional-scale studies B. Removal of area effect results in large elevational diversity shift C. Regional-scale studies should show more decreasing and low-elevation plateau diversity patterns than local-scale studies (standardized sampling area per elevation)
Mid-domain effect (MDE)	Unimodal diversity within a bounded domain; highest diversity at mid-point of domain	A. Elevational diversity unimodal on all mountains B. Empirical diversity at each 100-m band positively related to predicted diversity at that elevation C. Deviations of maximum diversity away from the mid-point of mountain are randomly distributed D. Strong, significant relationship between MDE model fit (r^2 value) and average species range size–domain size ratio
Climate I: temperature	Diversity positively related to temperature	A. Elevational diversity decreasing on all mountains B. Diversity at each 100-m band positively related to average annual temperature at that elevation C. No statistical difference between the temperature–diversity relationship on humid and arid mountains
Climate II: temperature and water (ECM*)	Diversity positively related to productivity†	A. Elevational diversity highest in warm, wet conditions: unimodal on arid mountains; decreasing or low-plateau on humid mountains. B. Diversity highly related to temperature on wet mountains, relationship weaker on arid mountains C. On arid mountains, maximum diversity occurs at wetter, cooler conditions than the mountain base
Evolutionary history	I = Diversity highest at elevation of max. speciation and colonization, min. extinction (static models) II = Evolutionary forces different on each mountain or region (historical contingency) III = Diversity highest in tropical conditions (warm, wet) within which most taxa speciated (niche conservatism)	I. Elevational diversity patterns similar on all mountains II. Each mountain has different elevational diversity pattern; or only regional mountains have consistent patterns III. Maximum diversity in warmest, wettest conditions; same prediction of ECM. Further testing requires complete phylogenies; currently unavailable
Interactions	I. Area–MDE II. Area–MDE–temperature III. Area–MDE–ECM	I. Area-corrected diversity improves fit to MDE II. Multiple regressions quantify relative contribution III. If area a primary factor in II above, then area-corrected data changes fit to MDE and ECM

*ECM = elevational climate model, see text for definition.

†Positive relationship with productivity and diversity would be the ideal montane hypothesis, but is currently not testable here given lack of sufficiently small-scale, global data for net primary productivity or precipitation.

100s of metres) data on water variables like rainfall and productivity; (2) lack of species-level, time-calibrated phylogenetic trees encompassing all the bird diversity for the montane gradients; and (3) lack of appropriately sampled biotic data (e.g. species abundances, competitive interactions). Nonetheless, the consistency of several proposed drivers can be powerfully tested using globally distributed elevational gradients

encompassing the variability in climate, area profiles and biogeographical history. Those factors showing a globally consistent signal have the greatest impact on global biodiversity, as seen for similar studies for non-flying small mammals and bats (McCain, 2005, 2007a,b). Bird elevational gradients may be an even more powerful test of diversity theories, since birds are a species-rich taxon and have been studied extensively on

mountains across the globe due to their visibility and predominantly diurnal nature. Here I examine global patterns for bird faunas along elevational gradients in various latitudes, climates and biogeographical regions. I detail the testable diversity hypotheses and their specific predictions for montane gradients. I then examine the consistency in which these diversity patterns correspond to the predictions of climate, space (area and MDE) and evolutionary history alone and in combination in an attempt to delineate the primary drivers of bird diversity globally.

MATERIALS AND METHODS

Bird elevational data

I found papers on bird elevational diversity by searching BIOSIS and Web of Science using various combinations of keywords: bird, avian, diversity, species richness, elevation(-al), altitude(-inal). Elevational diversity was also compiled from regional bird field guides and faunal surveys that included elevational ranges for each species (e.g. Inskipp *et al.*, 1999; Grimmett *et al.*, 2000; Robson, 2002; Hilty, 2003). Only studies surveying all birds, terrestrial birds, breeding birds or forest birds were used in the quantitative analyses. Studies examining only endemics or a particular bird guild (e.g. insectivores or thrushes) were not included. Endemic, elevational bird diversity will be treated in a separate paper (C.M. McCain, unpublished). If data were available in a single study differentiating breeding, forest and oceanic birds, summer and winter elevational ranges and/or different mountain slopes, then each of these datasets was analysed individually and compared. In the final analyses, breeding bird elevational ranges excluding oceanic birds were used preferentially if available. Only two datasets included altitudinal migrant elevations for winter and summer (Inskipp *et al.*, 1999; Grimmett *et al.*, 2000); both showed no difference in shape of the diversity pattern, although winter diversity decreased more rapidly with elevation than summer diversity in both studies.

Datasets were selected based on several *a priori* sampling criteria, since sampling is so important for detecting unbiased patterns in comparative analyses (McCain, 2005, 2007a; Rahbek, 2005; see Appendix S1). First, datasets were included in quantitative analyses only if sampling covered at least 70% of the elevational gradient. This is a critical restriction for studies with limited sampling at lower elevations, since discernment of pattern is strongly contingent on diversity estimates in the lowest 600 m. In contrast, limited sampling at the highest elevations is less critical since diversity always decreased monotonically above some threshold intermediate elevation. Second, sampling effort needed to be substantial and not biased strongly elevationally, although in practice this could be difficult to assess due to the highly variable nature of the explanations of sampling in the text of the studies. Third, assessments were made (or noted if discussed by authors) of elevational correlations in species richness with sampling intensity or wide-scale habitat disturbance (e.g. Taiwan). In cases where the authors stated there were elevations at the top or bottom of the mountain which were

undersampled, these elevations were not included in the analyses (e.g. the lowest 200 m in Bhutan, Inskipp *et al.*, 1999).

In reanalyses, I assumed that a species was present between its highest and lowest reported elevations (range interpolation). This improved methodological consistency, since most published accounts assumed range interpolation. Interpolation aids in overcoming some limitations of undersampling, but may also inflate estimates of species richness at mid-elevations (Grytnes & Vetaas, 2002). Species richness was then calculated based on the number of bird ranges occurring at each 100-m elevational band from the base to the top of the mountain (e.g. 0–99.9 m, 100–199.9 m, etc.) unless a larger resolution was used in a particular study without raw data for reanalysis. For those studies without species elevational range data, the bird diversity estimates at each surveyed elevation were taken from figures or tables in the publication.

For all gradients, species richness patterns were assigned to four categories: decreasing, low plateau, low plateau with a mid-peak and mid-elevation peak (see Fig. 1; more patterns were possible but only these four were necessary with current data). Decreasing richness patterns are those in which species numbers decline monotonically with increasing elevation. Low-plateau patterns have more than 300 m of consecutively high richness at the mountain base and thereafter decreasing species richness. Low-plateau patterns with a mid-peak have high richness across low elevations (> 300 m) with a diversity maximum found above 300 m from the base. Mid-elevation peaks have a unimodal peak in diversity at intermediate elevations (above 300 m) with 25% or more species than at the base and top of the mountain.

Elevational gradients were generally studied at two scales: local (alpha) or regional (gamma) species richness. Alpha richness refers to local samples taken from field transects along single elevational gradients. Gamma datasets are species richness patterns compiled from sighting and capture records, specimen records and field notes for an entire mountain or mountainous region regardless of slope, area or standardized trapping effort across elevations. Regional richness may be highly influenced by area (Rahbek, 1997, 2005; Brown, 2001; Lomolino, 2001; Willig *et al.*, 2003; McCain, 2005, 2007b), and may have significant sampling biases (Rickart, 2001). As the scale (grain) of the data in alpha and gamma patterns are qualitatively and quantitatively different, the factors producing these patterns may not necessarily coincide (McCain, 2005; Rahbek, 2005).

Diversity hypotheses and testing methods

Many hypotheses proposed to explain large-scale patterns in species richness apply to elevational richness patterns. Several are currently testable, including sampling, the species–area effect, the MDE, temperature, temperature and water (elevational climate model, ECM), a few theoretical constructs of evolutionary history and some combinations of these hypotheses (Table 1). Below I will detail each hypothesis, specify its elevational application, list its specific predictions and delineate appropriate methods for elevational bird analyses.

Sampling

Large differences in sampling effort across the gradient may result in an experimental bias in diversity estimation (e.g. Colwell & Coddington, 1994). In cases where elevational bands were sampled with unequal effort, a relationship between diversity and elevation could simply be a result of differential sampling effort. Two sampling predictions can be tested: (A) a positive correlation between bird diversity and a quantification of sampling effort (e.g. survey days, mist-net hours) across elevational bands; (B) local-scale studies that standardized sampling effort among elevations should show a significantly different distribution of elevational diversity patterns than non-standardized regional studies. Studies with major sampling biases and significant, positive correlations between elevational sampling effort and diversity were excluded. Exclusion was necessary because current analyses are conducted to delineate non-anthropogenic influences on bird diversity. A chi-square test of homogeneity determined if sampling methodology resulted in different frequency distributions of elevational diversity patterns between standardized local gradients and non-standardized regional gradients.

Area

The SAR asserts that as survey area increases the number of species encountered increases (Terborgh, 1973; Rosenzweig, 1992, 1995 and references therein). On mountains, the SAR predicts that elevational bands covering more area (e.g. mountain base) should harbour more species than elevational bands covering a small area (e.g. mountain tops) (Rahbek, 1997; McCain, 2007b). The SAR is based on the assumption that at regional and global scales extinction rates should decrease and speciation rates should increase with area due to the increased likelihood of barrier formation and increased population densities (Rosenzweig, 1995 and references therein). At small spatial scales, Rosenzweig (1995) argued that habitat diversity and the strong ties of particular species to habitat drive the local SAR. The elevational diversity patterns on mountains may fall somewhere on the continuum between these two scales and processes.

SAR prediction (A) is that studies at regional scales which amass diversity data across many sites at each elevation should show a positive relationship between bird diversity and elevational band area (Rahbek, 1997; McCain, 2007b). This was assessed by SAR regressions published in the original studies or by calculating SAR regressions for those datasets where both species richness data and area of elevational bands were available at the same scale from the published paper or earlier area studies (McCain, 2007b). In the latter case, area estimates for each 100-m elevational band were calculated using ArcGIS and digital elevation models at 90–100 m resolution or smaller (USGS data; see McCain, 2007b, for more details). I tested both a linear [no. of species = constant \times area ($S = cA$)] and a curvilinear ($\log S = z \log A + \log c$) area relationship. Regressions estimated the strength, slope and significance of the SAR (e.g. Conner & McCoy, 1979; Rosenzweig, 1995; McCain, 2007b).

SAR prediction (B) is that gradients with a significant, positive relationship between area and diversity, adjusting the species richness curve by standardizing for area should result in a large change in the elevational diversity pattern (McCain, 2007b). Area standardization was based on calculating area-corrected diversity curves using the power function ($S = cA^z$; e.g. Conner & McCoy, 1979; Rosenzweig, 1995) with a comparison of two z -values: a z -value based on the slope of log–log SAR regressions and the canonical z -value (0.25) proposed by Preston (1962). Area adjustment simply involves solving the power function equation for the constant (c) after plugging in known values for z , number of species and area estimate at each 100-m elevational band. This is simply an area correction that calculates the expected diversity at each elevation if the amount of area was held constant among elevational bands, given the known logistic relationship between diversity and area. These corrections are not reanalyses of the area residuals from SAR regressions, so avoid pitfalls inherent in analyses of residuals (e.g. Freckleton, 2002). Previous work compared several techniques for area correction and estimation of parameters, and found that most correction techniques produce highly correlated results, but supported the technique used here as the most robust (McCain, 2007b).

SAR prediction (C) is that regional-scale studies should display more decreasing and low-elevational plateau patterns, since land area is generally highest toward the base of mountains, than local-scale studies which sampled small plots of relatively standardized area per elevation. A chi-square test of homogeneity tested for a significantly different frequency distribution in elevational diversity patterns between standardized local gradients and regional gradients.

Mid-domain effect (MDE)

The MDE assumes that spatial boundaries (e.g. the base and top of a mountain) cause more overlap of species ranges toward the centre of an area where many large- to medium-sized ranges must overlap but are less likely to abut an edge of the area (Colwell *et al.*, 2004, 2005 and references therein). On mountains, MDE predicts (McCain, 2004) (A) a unimodal diversity curve with maximum diversity at the mid-point of the mountain. A chi-square goodness of fit test assessed whether there are significantly more mid-elevation peaks than any other diversity pattern. Additionally, the MDE predicts (B) a strong, positive association between predicted diversity based on Monte Carlo simulations (Mid-Domain Null; McCain, 2004) and empirical diversity at each 100-m elevational band. Mid-Domain Null simulates species richness between the mountain base and the summit based on random placement of empirical range sizes sampled without replacement (McCain, 2004). Regressions of empirical and predicted values, based on the average of 50 000 simulations at each 100 m elevational band give r^2 estimates of MDE fit (Colwell *et al.*, 2004; McCain, 2004).

Two secondary predictions of MDE are testable. MDE predicts (C) that deviations in maximum diversity away from the mid-point of the mountain should be randomly distributed if

spatial constraints alone drive elevational diversity (e.g. area or climate is not directionally skewing the diversity peak away from the mid-point of the mountain; Student's *t*-test). Lastly, MDE predicts (D) a strong, significant relationship between MDE fit (r^2 value) and a ratio of the average bird range size to elevational gradient length. This is based on the premise that MDE predictions are based mainly on the overlap of medium- and large-ranged species, and do not apply necessarily to small-ranged species; thus gradients with more large-ranged species should show better fits to MDE (Lees *et al.*, 1999; Colwell *et al.*, 2004; Dunn *et al.*, 2007). Linear regressions of MDE r^2 values with a ratio of average bird range size (m) divided by the length of the elevational gradient (m) for each study will assess the strength of MDE range size prediction (Lees *et al.*, 1999; Dunn *et al.*, 2007).

Climate I: temperature

Climatic tolerances put restrictions on how many species can survive at different locations and elevations (e.g. Brown, 2001; Hawkins *et al.*, 2003b). A positive relationship between temperature and diversity has been shown for many large-scale diversity patterns, although hypotheses about the underlying mechanism differ (Pianka, 1966; Kaspari *et al.*, 2000; Allen *et al.*, 2002; Hawkins *et al.*, 2003b; Evans *et al.*, 2005; Sanders *et al.*, 2007). On mountains, temperature decreases monotonically by an average of 0.6 °C per 100-m elevational gain (Barry, 1992). If temperature is a main determinant of bird diversity, the predominant elevational diversity pattern predicted is decreasing diversity with decreasing temperature and increasing elevation (prediction A; chi-square goodness of fit test). Specifically (B), bird diversity in each elevational band should be significantly and positively correlated with temperature on all montane gradients in linear regressions. Because each study did not publish temperature variation with elevation, the average annual temperature for the lowest 100 m was taken from the WorldClim database (1 km² scale; <http://www.worldclim.org/>), and for standardization assumed to decrease by 0.6 °C per 100-m elevation gain (Barry, 1992). Lastly (C), this positive temperature–diversity relationship should not differ among mountains in different climatic regimes, in particular arid mountains and wet-forested mountains should show equally strong relationships with temperature. The equality of r^2 values between arid and wet mountains is compared with a nonparametric, Mann–Whitney *U*-test.

Climate II: temperature and water

Climatic productivity has also been strongly and positively linked to diversity (O'Brien, 1993; Gaston, 2000; Kaspari *et al.*, 2000; Mittelbach *et al.*, 2001; Hawkins *et al.*, 2003a,b; Evans *et al.*, 2005). Several mechanisms attempt to explain this relationship and are nicely summarized in Evans *et al.* (2005); many of these are not testable directly here due to a lack of abundance data and small-scale productivity/water data. However, an elevational climate model (ECM) was recently proposed and supported for bats (McCain, 2007a), wherein separate gradients in temperature

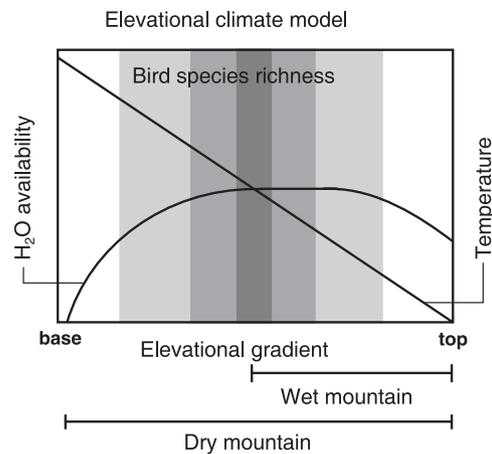


Figure 2 Elevational climate model for bird species richness, incorporating a linearly decreasing temperature gradient and a unimodal water availability gradient. Bird species richness is depicted in grey tones with darker tone indicating more species. The placements of generalized wet and dry montane gradients are shown below the x-axis. Unimodal mid-elevational peaks in bird diversity are predicted on dry mountains and decreasing or low-plateau patterns predicted on wet mountains.

and water availability on mountains in different climatic regimes predict divergent elevational diversity patterns (Fig. 2). Temperature decreases with elevation on all mountains, while rainfall and water availability follow more complex relationships with elevation depending on the local climate. On arid mountains (e.g. south-western US mountains), water availability is highest at intermediate elevations where rainfall and soil water retention are highest and evaporation lowest. Water availability drops off dramatically towards the low elevations where high temperature and high evaporation exceed rainfall inputs, leading to arid habitats. Towards the upper elevations water availability also drops toward the mountaintop, although less dramatically, as runoff is high due to shallow soils and exposed rock, and precipitation is seasonally inaccessible as snow and ice. On humid mountains (e.g. the eastern Andes), water availability is high across a broad base of lower elevations and only decreases toward the tops of the mountains, again due to higher runoff and decreases in rainfall.

Bird species richness is predicted to be positively related to the warmest and wettest conditions elevationally, predicting (A) mid-elevation peaks in bird species richness on arid mountains and decreasing diversity on warm, wet mountains (Fig. 2). Each elevational gradient is assigned to an arid or humid mountain classification based on vegetation present at the base of the mountain: arid includes hyper-arid, arid, and semi-arid vegetation types (humidity index < 0.50; UNEP, 1997, World Atlas of Desertification classification) and humid mountains include various forest vegetation types (> 0.50 humidity index). A chi-square test of homogeneity is used to assess whether particular diversity patterns are more associated with a particular base climate than random. ECM prediction (B) is that temperature should show a stronger relationship with bird diversity on

mountains in humid climates, than with bird diversity on mountains in arid climates (linear regressions and Mann–Whitney *U*-test). Finally, on arid mountains (prediction C), the mid-elevation climatic conditions at the diversity maximum should be wetter and cooler than at the mountain base. Climate conditions were estimated using annual precipitation and temperature from the WorldClim database (1 km² scale; <http://www.worldclim.org/>). These data do not include differences in evaporation or runoff and are at a coarser scale than most elevational variation, so will underestimate the actual differences in water availability. However, these data may provide additional support to ECM if maximum bird diversity on arid mountains occurs at mid-elevations that are statistically wetter and cooler than conditions at the mountain base even if underestimated (paired *t*-test).

Evolutionary history

Evolutionary rates hypotheses are less developed elevationally than latitudinally, although recent analyses are forging new ground (e.g. Wiens *et al.*, 2007). Due to a lack of species-level time-calibrated phylogenetic trees and speciation/extinction rate data for each mountain, many phylogenetic trends like the time-for-speciation effect are not testable here (Stephens & Wiens, 2003; Wiens *et al.*, 2007). But some general, simplistic predictions can be examined. These tests are weaker than those for climate and space, but will emphasize the critical characteristics that an evolutionary hypothesis would need to be globally supported for birds. Static evolutionary models (prediction A) propose a region on mountains where conditions promote speciation and dampen extinction risk, and therefore predict a single diversity optimum. For example, if speciation is highest at the mountain base and declines with elevation, and extinction is highest at the mountaintop and decreases toward the base, then the evolutionary optimum for diversity would occur at mountain bases globally. A single, consistent diversity optimum is the general prediction of all static evolutionary models proposed to date (e.g. Brown, 2001, p. 107; Heaney, 2001, hypothesis 12; Lomolino, 2001, Fig. 3). If evolutionary factors generating montane diversity are strongly contingent on local fauna, conditions and biogeographical history, then no consistent, global signals in elevational diversity are predicted (prediction B). Such a historical contingency would predict a lack of consistent patterns globally or only regionally consistent patterns. Lastly (prediction C), niche conservatism proposes that climatic conditions within which a taxon evolved – tropical-like conditions for most modern groups and species – should be conserved in the present (Wiens & Donoghue, 2004). Thus, the basic elevation trend that niche conservatism predicts is maximum bird diversity in the warmest, wettest conditions on mountains; the same general pattern as that of ECM.

Interactions

Three hypothesis interactions can be tested for variables quantified at the same scale as bird diversity (e.g. 100-m elevational

bands): area, MDE and temperature. (I) Interaction of area and MDE, maximum diversity may be consistently skewed away from the mountain mid-point toward the portion of the mountain covering the most area. Such a relationship predicts that once diversity has been standardized for area (area-corrected diversity curves: area prediction B), then the fit to MDE should be significantly improved. This interaction will be tested with a nonparametric, Mann–Whitney *U*-test to see if MDE *r*² values for area-corrected diversity are higher than MDE *r*² values for empirical diversity. (II) Interaction of area, MDE, and temperature can all be simultaneously tested using multiple regressions to assess the relative contribution of each factor. Finally (III), if area is more important to bird diversity than temperature and MDE in multiple regressions, then the precedence of the area effect is established. In that case, area-corrected diversity curves can be used to reassess the fits of ECM and MDE. Lastly, spatial autocorrelation exists both in the bird elevational diversity and environmental data, which may influence the results of these analyses, although not necessarily (Diniz-Filho *et al.*, 2003; Hawkins *et al.*, 2007b). Due to the length and complexity of current analyses, spatial autocorrelation analyses and influences of multiple tests (e.g. Bonferroni corrections) need to be treated in a separate paper.

RESULTS

I found 190 elevational gradients of bird species richness in 150 published studies. Only 78 gradients met *a priori* sampling criteria and had independent robust content for quantitative analyses (see Appendices S1 and S2 in Supporting Information). These gradients cover mountainous regions from various climates (tropical, subtropical, arid, temperate), latitudes (24.5° S to 48.2° N), longitudes (119.8° W to 147.3° E), landmasses (islands and continents), mountain heights (851 m to 8848 m) and scales (local and regional) (Figs 3 & S1). Four elevational diversity patterns were represented (Fig. 1a): 29% decreasing, 19% low-elevation plateaus, 26% low-elevation plateaus with mid-peaks and 26% unimodal with mid-peaks. This distribution of diversity patterns was the same for studies of all birds (*n* = 28), terrestrial birds (*n* = 8), breeding birds (*n* = 28) or forest birds (*n* = 14) ($X^2 = 8.143$, d.f. = 9, *P* = 0.5198). Continents and islands generally showed the same patterns, although islands showed fewer mid-peaks mainly since they were predominantly tropical (see results below). There was no relationship between elevational diversity and mountain height ($r^2 = 0.015$, *P* = 0.282, *n* = 78), or latitude ($r^2 = 0.040$, *P* = 0.079, *n* = 78). Tests of the predictions of each diversity hypothesis and interactions (Table 1) are detailed sequentially below:

Sampling

No distinct sampling trends existed once biased datasets were removed. No differences were detected in diversity patterns based on sampling protocol between standardized local and non-standardized regional-scale studies (prediction B; Fig. 1b; $X^2 = 3.03$, d.f. = 3, *P* = 0.387, *n* = 78).

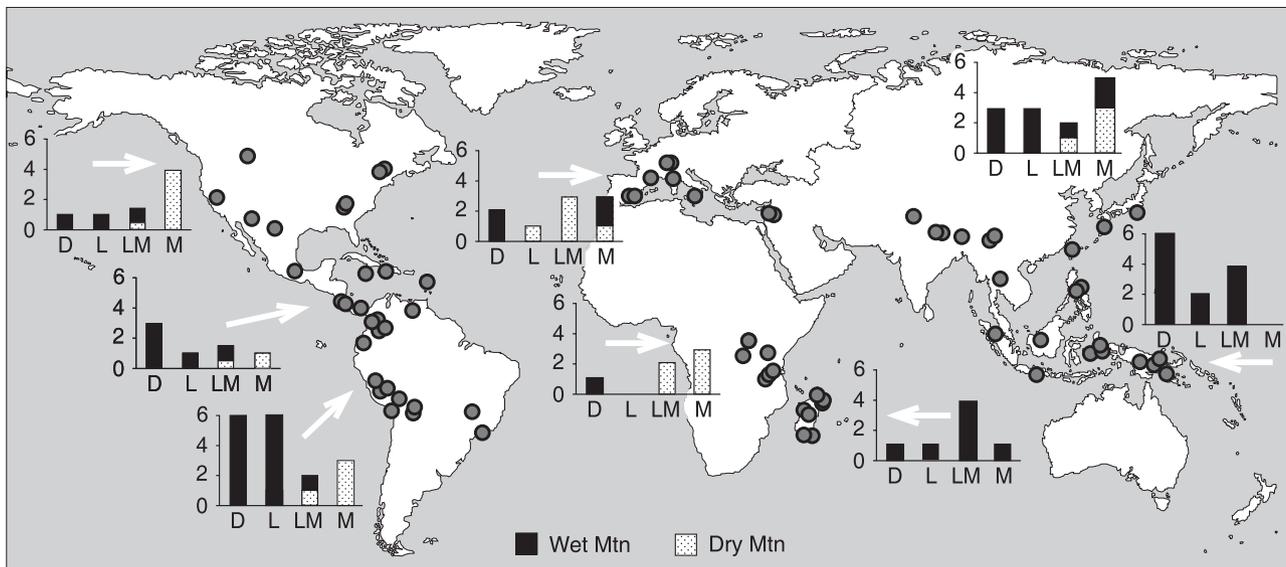


Figure 3 The distribution of study sites (circles), the four main elevational richness patterns for each geographical region (bars) and the number of patterns on wet- and dry-based mountains (dark and stippled, respectively): North America, Central America, South America, Europe, continental Africa, Madagascar, Asia and Australasia. D = decreasing, L = low plateau, LM = low plateau with mid-elevational peak, M = mid-elevational peak (see text for definitions).

Area

Support for the three area predictions was mixed. Positive, significant SARs (prediction A) were detected in 16 of 22 studies with appropriate data either in linear or curvilinear analyses: average r^2 values of 0.29 and 0.63, respectively (Fig. 4a, Table S1). Significant shifts in diversity pattern with area-corrected diversity curves occurred in 12 of 16 significant gradients (prediction B): 4 showed little change from the empirical diversity curve, 11 showed an upward shift in maximum diversity to a mid-elevational peak, and 1 shifted to a low-elevation plateau (Table S1). As shown in previous studies (McCain, 2007b), these analyses are robust to methodological and parameter variation. Lastly (prediction C), regional-scale studies with a proposed larger species–area influence did not show a preponderance of decreasing or low-plateau diversity patterns compared with local studies with area standardization (Fig. 1b; $X^2 = 0.002$, d.f. = 1, $P = 0.9643$, $n = 38$).

Mid-domain effect

Bird diversity had low concordance with the four MDE predictions. Elevational diversity was not uniformly unimodal (contrary to prediction A). Fits to the null model were generally poor: 0.192 average r^2 value for those studies with available species range data (prediction B; Fig. 4b; $n = 43$; Appendix S1). Local gradients had higher average r^2 values than regional gradients (0.344 and 0.126, respectively), mainly due to slightly more mid-peaks found in local-scale studies (although not significantly more). Deviations in maximum bird diversity were not randomly distributed around the mountain mid-point, but were shifted to significantly lower elevations (prediction C; $t = -7.10$,

$P < 0.0001$, $n = 43$). Lastly, there was a positive relationship between average bird range size relative to gradient length and fit to MDE (r^2 value), although the overall relationship was not particularly strong for all gradients ($r^2 = 0.274$, $P = 0.0003$, $n = 43$) or for just those with MDE predicted mid-peaks ($r^2 = 0.260$, $P = 0.0183$, $n = 21$).

Climate I: temperature

Support for the three temperature predictions was mixed. Bird diversity did not exhibit predominantly decreasing and low-plateau patterns as predicted by decreasing temperature on mountains (prediction A). Bird elevational diversity was positively and significantly related to temperature on 65 of 76 gradients with testable data, although the strength of the relationship was highly variable ranging from r^2 values of 0 to 0.98 (prediction B; Fig. 4c; Appendix S1). Contrary to temperature predictions (prediction C), the strength of the temperature–diversity relationship was contingent upon local climate (humid average $r^2 = 0.807$, arid average $r^2 = 0.496$; Mann–Whitney U -test: $Z = 15.74$, $P < 0.001$, $n = 76$).

Climate II: temperature and water (ECM)

The three predictions of ECM were all consistently supported. All decreasing and most low-plateau diversity patterns occurred on wet mountains, and the majority of mid-peak patterns were from dry mountains (prediction A; Fig. 5a; $X^2 = 30.79$, d.f. = 3, $P < 0.0001$). The trend was strongest in the western hemisphere (Fig. 5b; $X^2 = 84.70$, d.f. = 3, $P < 0.0001$), but was significant in the eastern hemisphere, most biogeographical regions (Fig. 3, Fig. S1), and separately for breeding bird

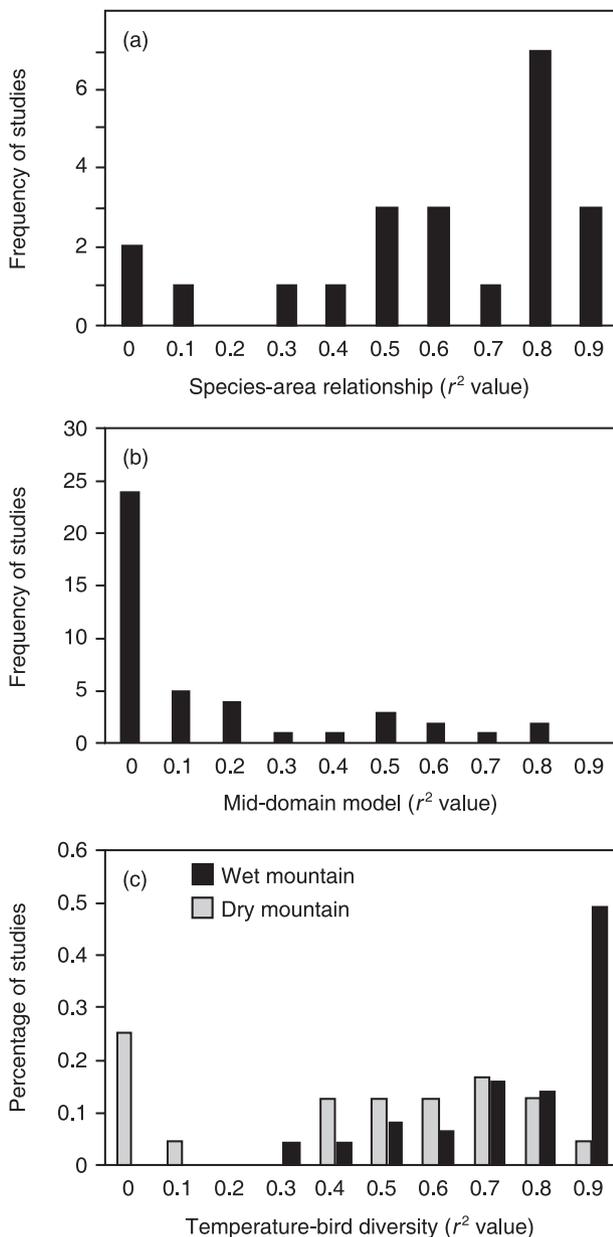


Figure 4 Regression analyses of the species–area, mid-domain and temperature–diversity relationships using elevational patterns in bird diversity: (a) Fits to the log–log species–area relationship ($n = 22$) with an overall mean r^2 of 0.634. (b) Fits to the mid-domain model ($n = 43$) with an overall mean r^2 of 0.192. (c) Fits to the temperature–bird diversity relationship with an overall mean r^2 of 0.710, contrasting humid and dry mountain relationships ($r^2 = 0.807$, $n = 51$; $r^2 = 0.496$, $n = 24$, respectively).

gradients (Fig. 5c; $X^2 = 73.79$, d.f. = 3, $P < 0.0001$) and local gradients (Fig. 5d; $X^2 = 13.47$, d.f. = 3, $P = 0.0037$). As predicted (prediction B), the temperature–diversity relationship was stronger on humid rather than dry mountains. This trend was also supported when only considering patterns with mid-peaks [LPMP: $Z = 4.56$, $P < 0.001$; MP: $Z = 8.42$, $P < 0.001$]. Even with coarse climatic data (prediction C), maximum bird diversity on

arid mountains was located in significantly wetter and cooler conditions than at the mountain base (Fig. 6; rainfall: paired $t = 2.66$, $P = 0.007$, $n = 23$; temperature: paired $t = -8.55$, $P < 0.0001$, $n = 23$).

Evolutionary history

Of the three general predictions of historical factors underlying elevational diversity, only niche conservatism was supported. There appears to be no single optimum in species diversification on mountains (theory I: static models), since there are four distinct trends in elevational diversity. Similarly, diversity patterns were neither ubiquitously different nor regionally consistent (theory II: historical contingency), but varied within regions due to local climatic conditions. The warm, wet climates under which birds are purported to have diversified consistently do harbour the most species on mountains, thus supporting the simplest prediction of niche conservatism (theory III).

Interactions

An area–MDE interaction was not supported (interaction I). There was no significant increase in MDE fit when calculated with area-corrected bird diversity with either z -value, as mean r^2 values were nearly identical: empirical = 0.134, mountain $z = 0.131$, z of 0.25 = 0.139 (Mann-Whitney U -test (mountain z): $Z = 0.624$, $P = 0.268$, $n = 11$; ($z = 0.25$) $Z = 0.295$, $P = 0.386$, $n = 11$). Multiple regression analyses of area, temperature and MDE with bird elevational diversity tested with each 100 m elevational band (interaction II; all variables log-transformed for normality) found all three factors significant in the final model [$r^2 = 0.7211$, F ratio = 441.72, $P < 0.001$, $n = 542$ (elevation bands)] with temperature contributing the most to the model ($r^2 = 0.2343$), followed by MDE ($r^2 = 0.1176$), then area ($r^2 = 0.0554$). Because area in the multiple regressions was shown to be the factor with the least importance, there is no statistical or biological foundation for testing interaction III.

DISCUSSION

In the not so distant past it was thought that all diversity patterns of birds, in fact all faunal and floral groups, decreased with increasing elevation (e.g. MacArthur, 1972; Terborgh, 1977; Brown & Gibson, 1983; Brown, 1988; Rohde, 1992; Stevens 1992). Rahbek (1995) falsified this assumption by showing that many elevational gradients have mid-elevational peaks in diversity. This bird analysis shows conclusively using all available and well-sampled datasets that neither decreasing nor mid-elevational peaks are the sole predominant pattern for birds on mountains. Bird diversity follows four general patterns in nearly equal frequency: decreasing, low plateau, low plateau with a mid-elevation peak and unimodal with a mid-elevational peak (Fig. 1). These patterns are seen across all comprehensive bird assemblages (all, terrestrial, breeding or forest birds), across both the eastern and western hemispheres, and within each biogeographical region (Figs 3 & S1). This elevational variability may be attributable

Figure 5 The elevational climate model (ECM), based on temperature and water availability, predicts maximum bird richness at mid-elevations on dry mountains, and decreasing and low plateaus in bird richness of wet mountains. ECM was statistically supported across the robust elevational gradients in bird species richness: (a) all localities ($X^2 = 30.8$, d.f. = 3, $P < 0.0001$), (b) western hemisphere ($X^2 = 84.7$, d.f. = 3, $P < 0.0001$), (c) breeding birds ($X^2 = 73.8$, d.f. = 3, $P < 0.0001$), (d) local-scale gradients ($X^2 = 13.47$, d.f. = 3, $P = 0.0037$). Low Plateau (MP) refers to low plateaus with mid peaks.

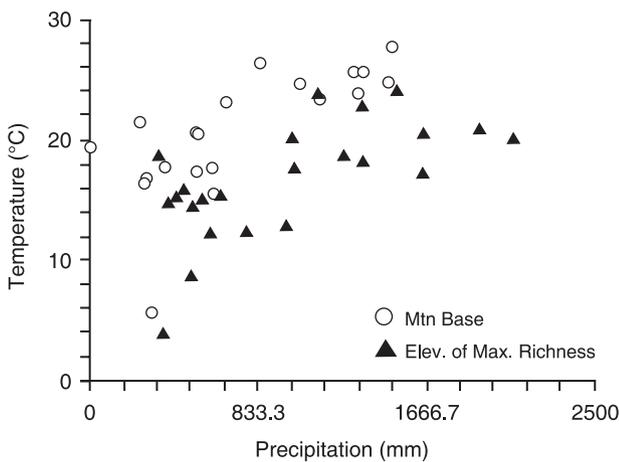
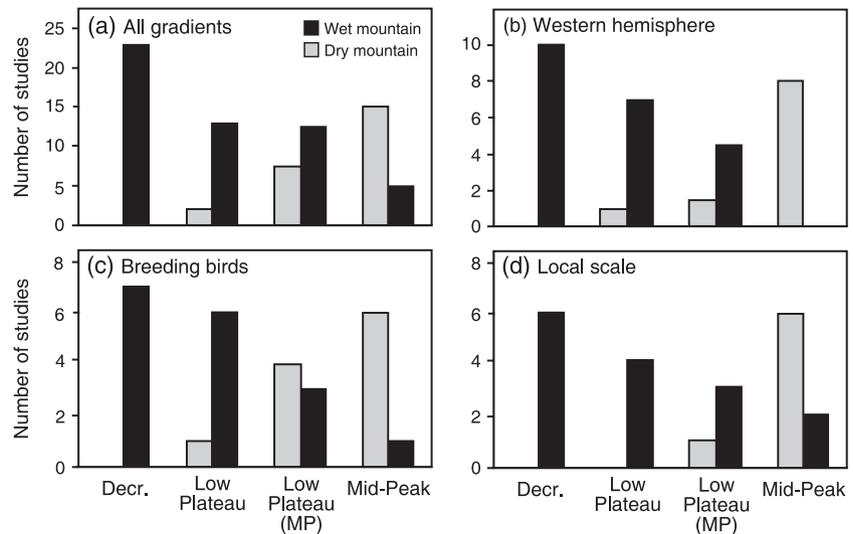


Figure 6 A contrast of climate conditions (average annual precipitation and temperature) at the mountain base and at the mid-elevation with maximum bird richness on arid mountains. Bird diversity occurs at significantly wetter (paired $t = 2.66$, $P = 0.007$) and cooler (paired $t = -8.55$, $P < 0.0001$) conditions at higher elevations on dry mountains (WorldClim data; pixel scale = 1 km²).

to particular proposed drivers of global biodiversity, including sampling, spatial, climatic or evolutionary factors (Table 1), but is the support for any of these consistent enough to be globally persuasive?

Sampling

Robust patterns in bird elevational diversity are not due to sampling bias. After the removal of studies with obvious sampling biases, there was no sampling signal in diversity patterns between standardized and non-standardized studies. Additionally, sampling simulations conducted on elevational diversity patterns found that unrealistically large changes in a significant proportion of the species ranges are necessary to change overall diversity patterns (e.g. an average error of 2000–

3000 m in range sizes; McCain, 2007a). Simulations showed undersampling insufficient to change most decreasing patterns to a mid-peak, unless 25–50% of species occurring on a mountain are currently unknown and with ranges that occur only at intermediate elevations (McCain, 2007a). Such vast numbers of unknown bird species and huge range underestimations for large percentages of the birds on each mountain are highly unlikely with our current distributional knowledge of birds. Additionally, it would be very difficult to associate differential sampling biases to the dichotomous diversity trends seen on humid and arid mountains.

Area

Some predictions of the SAR were supported for montane birds: many studies showed a significant, positive relationship between elevational bird diversity and elevational area, and more than half of the significant SAR studies showed substantial change in the elevational diversity pattern with area corrections (Fig. 4a, Table S1). Whereas other SAR predictions were not supported, regional-scale studies, many with large area effects, did not show significantly more decreasing or low plateaus in diversity than area-standardized, local-scale studies (Fig. 1), and area had the least influence on bird diversity after temperature and MDE in combined multivariate analyses (interaction II).

Mixed support for the area effect on mountains is consistent with similar analyses of non-flying mammals and bats (McCain, 2007b). Like in birds, strong area effects were detailed for only half of the mammalian gradients. Other taxonomic groups also show mixed SAR effects on mountains: supportive (plants: Jones *et al.*, 2003; Bachman *et al.*, 2004; ants: Sanders, 2002; fish: Fu *et al.*, 2004) and not supportive (plants: Odland & Birks, 1999; Vetaas & Grytnes, 2002; Bhattarai *et al.*, 2004; Oommen & Shanker, 2005; ants: Sanders *et al.*, 2003). Generally, strong correlations with area occur on mountains with decreasing or low plateau diversity, but infrequently with low plateaus with mid-peaks and unimodal patterns in diversity (Table S1; McCain, 2007b). These mixed results warrant two main

conclusions. First that area, which on most mountains decreases with increasing elevation, tends to be correlated with the decreasing temperature effect on mountains, and for montane birds, temperature was shown to be the stronger of the two effects in multiple regressions. Second, the fact that many bird gradients showed a negative or no relationship with area, and no large differences existed between regional- and local-scale studies shows conclusively that area cannot be the main driver of bird elevational diversity, only a factor of secondary importance. For that reason, I caution against methodologies promoting the initial removal of area effects before examining other potential drivers of diversity (e.g. Rahbek, 1997; see Freckleton, 2002).

Mid-domain effect (MDE)

Spatial constraints on species ranges are theoretically implicated and, in some cases, cannot be rejected as a contributing factor to mid-elevational peaks in species richness (e.g. Colwell *et al.*, 2004, 2005; but see Hawkins *et al.*, 2005; Zapata *et al.*, 2005). The MDE predicts unimodal species richness with a maximum at the mid-point of all elevational gradients, but montane bird assemblages were not predominantly unimodal (Fig. 1). In fact, none of the four MDE predictions were strongly supported. The vast majority of MDE regressions found low fits to MDE predictions (average $r^2 = 0.192$; Fig. 4b, Appendix S1). And deviations of maximum diversity away from the mountain mid-point were significantly skewed toward lower elevations, not randomly distributed as expected. There was a positive relationship between average bird range size and the MDE fit, but the relationship was weak ($r^2 = 0.27$), nearly the strength of the average MDE fit. Lastly, MDE fits were not improved when area and MDE were tested together. Similar trends in low MDE fits, skewed deviations and lack of an area–MDE interaction were documented along elevational gradients globally for non-flying small mammals ($r^2 = 0.238$; McCain, 2005, 2007b) and bats ($r^2 = 0.156$; McCain, 2007a,b). For most vertebrate groups and other taxa examined so far (e.g. Dunn *et al.*, 2007), elevational patterns are not directly consistent with MDE. Thus, the main drivers of elevational bird diversity do not include either spatial variable considered here, SAR or MDE.

Climate

Support for the temperature model was mixed, reflecting that temperature alone is not responsible for the distribution of elevational diversity patterns in birds. I did not find a predominance of decreasing or low plateaus in bird diversity on mountains, and the temperature–diversity relationship was significantly stronger on humid mountains than dry mountains (Figs 1 & 4c, Appendix S1). Temperature had the strongest effect in multivariate analyses, but still a substantial portion of variation in diversity remained unexplained. Both water and temperature variables are needed to explain montane bird diversity.

Temperature–water predictions of the elevational climate model (ECM; Fig. 2) were the only set of predictions that were

uniformly and strongly supported (Figs 3, 4c, 5 & 6). Maximum bird diversity occurred at mid-elevation on dry mountains and at low elevations on humid mountains as predicted (Figs 3 & 5). Temperature was more strongly linked to diversity on wet mountains than on dry mountains (Fig. 4c). On arid mountains, maximum bird diversity occurred at significantly wetter and cooler climatic conditions at mid-elevations than climatic conditions at the base of the mountain (Fig. 6), even with underestimates of water availability. These results emphasize that water in a necessary factor modifying the temperature effect on elevational diversity.

Montane bats also strongly supported ECM: bat diversity was always unimodal on dry mountains and always decreasing on humid mountains except for a single exception which simulations show may be undersampled at low elevations (McCain, 2007a). Additionally, water and energy/temperature are correlated with elevational species richness of epiphytes (Krömer *et al.*, 2005) and ferns (Bhattarai *et al.*, 2004; Kluge *et al.*, 2006). A positive relationship between species richness and water and energy regimes has previously been demonstrated for woody plants across southern Africa (O'Brien, 1993) and across multiple large-scale geographical studies for plants and animals (Hawkins *et al.*, 2003b, and references therein). Clearly, water and energy regimes are essential to the physiology of plants and directly influence distribution and species richness (O'Brien, 1993; Hawkins *et al.*, 2003b; Bhattarai *et al.*, 2004; Krömer *et al.*, 2005; Kluge *et al.*, 2006). For animal richness patterns, the focus becomes the relative importance of direct (physiological limitations) and indirect (food resource) effects of water and temperature on diversity (Hawkins *et al.*, 2003b; McCain, 2007a).

Endothermic physiological constraints of birds may directly limit their ability to sustain populations at cold temperatures or high aridity (e.g. Root, 1988a,b; Weiner, 1992, and references therein). These energetic constraints are thought to act as a 'filter barrier' to upward or downward elevational range expansion, and result in the hard limits of bird distributions (e.g. Heaney, 2001). Cold temperatures clearly limit montane bird distributions, as fewer than 20 species were found at the highest elevations (> 75% mountain height). Temperature and water availability could also influence bird species richness indirectly through food resources and availability (e.g. Terborgh & Weske, 1975; Terborgh, 1977; Root, 1988b; Loiselle & Blake, 1991). Insect abundance, fruit and nectar production, and abundances of many small vertebrates are all predicted to be low in cold temperature regimes (e.g. Janzen, 1973; Janzen *et al.*, 1976; Fauth *et al.*, 1989; Loiselle & Blake, 1991; Navas, 2003), and low or patchy in arid conditions (e.g. Noy-Meir, 1973; Janzen, 1973; MacMahon, 1997; Perrin & Boyer, 2000). The optimal conditions for bird species richness – warm and wet – may be the most optimal conditions for production of their food resources. More studies addressing food resource distributions, bird resource use and physiological adaptations of bird species along elevational gradients are needed to tease apart the physiological and resource contributions to elevational diversity and distributional patterns.

Evolutionary history

The four distinct patterns in bird elevational diversity negated the possibility of a single evolutionary optimal from static models or ubiquitously divergent patterns in montane diversity from local historical contingencies. The latter was not due to high species overlap among mountains. Very few species were shared among mountains in the various biogeographical regions (0–7.7% species overlap), and predictably the amount of overlap decreases with distance (Table S2). Most evolutionary hypotheses on mountains are static, meaning that the factors thought to enhance speciation and immigration, and decrease extinction, are proposed to be the same for all mountain systems (e.g. Brown, 2001; Heaney, 2001; Lomolino, 2001). For example, Lomolino (2001) proposed that diversity should be higher at the base of mountains where immigration is higher. Diversity should then decrease with elevation as immigration rate declines with increasing isolation of high-elevation communities. This hypothesis would predict decreasing diversity on all mountains; hence it is a static diversity prediction. This analysis for birds shows unequivocally that static evolutionary models will not be supported for birds. Future evolutionary models, to be globally persuasive, will need to be tied to evolutionary trends that are different on humid and arid mountain systems. This is the case for niche conservatism (Wiens & Donoghue, 2004) and why it is the only evolutionary prediction that has initial support for birds.

Niche conservatism posits that most large-scale richness patterns result from taxonomic groups diversifying when the majority of the earth was dominated by a tropical-like climate (Wiens & Donoghue, 2004). If most birds evolved niches in warm, wet conditions then bird diversity should be concentrated at warm, wet elevations on mountains. This is supported here elevationally (see ECM) and previously latitudinally (e.g. Hawkins *et al.*, 2003a, 2007a). But so far, this result just emphasizes that montane bird diversity patterns are consistent with the basic tenet of niche conservatism. To directly test niche conservatism in future studies, time-calibrated phylogenies are needed to examine whether the oldest species are concentrated in the areas of highest diversity and whether niches of those species are more constrained to warm, wet conditions than are younger species across all of these mountain systems (e.g. Stephens & Wiens, 2003; Wiens *et al.*, 2006, 2007).

In summary, both water and temperature variables are needed to comprehensively predict the various elevational diversity patterns seen for birds. More analyses are needed to discern whether the mechanism underlying these relationships is ecological, based on physiological or food resource limitations, or historical, based on phylogenetic niche conservation or other evolutionary trends tied to climate. Two issues remain unresolved: why do some humid mountains show mid-elevational peaks in diversity and what explains the existence of low-elevation plateaus in dry climates? Most of the mid-peak outliers occurred in humid regions with high human disturbance over long time periods, for instance Taiwan, China and Madagascar. In fact, almost all of the Madagascan bird gradients are decreasing or low plateau if only sampled within intact habitats (e.g. Goodman *et al.*, 1997;

Hawkins, 1999; Goodman *et al.*, 2000). Similarly, studies in Taiwan and China found strong impacts of disturbance and human habitation at low elevations (Lan & Dunbar, 2000; Shiu & Lee, 2003; Lee *et al.*, 2004). But in general, the low elevations on arid mountain gradients were relatively undisturbed anthropogenically due to the low productivity and hence low human populations in these areas. Mid-elevational peaks also occur on elevational gradients in highland valleys of wet mountainous regions (e.g. the Prattigau Valley, Switzerland). In these cases, the typical low-elevation bird fauna of the regional elevational gradient may be missing or reduced, thus making the occurrence of a mid-elevational peak more likely. Finally, low-elevation plateaus in dry climates (e.g. Tanzania; Corsica, France) have a large portion of species that range across most of the lower and mid-elevations. In fact, the length of the plateau is longer in dry climates than wet climates globally (1373 m vs. 997 m; 47% vs. 29% of mountain height, respectively). Teasing apart the causes of low plateaus in bird diversity further requires more information of water availability curves and area profiles, which is currently unavailable, but will be a fruitful future direction. Lastly, high biodiversity on mountains underlines the need for current protection plans in montane regions to encompass large intact gradients in elevation and climate. Those montane bird faunas most at risk from global climate change are those where maximum diversity is at mid-elevations, including mountains in arid environments and those already devastated by low-elevation habitat destruction.

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SUPPORTING INFORMATION

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

Figure S1 Colour version of Fig. 3. Global map of the distribution of study sites and four elevational richness patterns of birds.

Table S1 Area analyses of bird elevational gradients.

Table S2 Number and percentage of bird species shared among mountains in different biogeographical regions.

Appendix S1 List, characteristics and citations of robust and informative elevational gradients used in analyses of bird species richness.

Appendix S2 Literature cited for gradients not used in elevational bird analyses.

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BIOSKETCH

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