INVITED REVIEWS AND SYNTHESES

# Environmental harshness is positively correlated with intraspecific divergence in mammals and birds

CARLOS A. BOTERO,*† ROI DOR,‡§ CHRISTY M. MCCAIN‡ and REBECCA J. SAFRAN‡
*Initiative in Biological Complexity, North Carolina State University, Raleigh, NC 27695, USA, †Southeast Climate Science Center, North Carolina State University, Raleigh, NC 27695, USA, ‡Department of Ecology & Evolutionary Biology, University of Colorado, Boulder, CO 80309, USA, §Department of Zoology, Tel Aviv University, Tel Aviv 6997801, Israel

## Abstract

**Life on Earth is conspicuously more diverse in the tropics. Although this intriguing geographical pattern has been linked to many biotic and abiotic factors, their relative importance and potential interactions are still poorly understood. The way in which latitudinal changes in ecological conditions influence evolutionary processes is particularly controversial, as there is evidence for both a positive and a negative latitudinal gradient in speciation rates. Here, we identify and address some methodological issues (how patterns are analysed and how latitude is quantified) that could lead to such conflicting results. To address these issues, we assemble a comprehensive data set of the environmental correlates of latitude (including climate, net primary productivity and habitat heterogeneity) and combine it with biological, historical and molecular data to explore global patterns in recent divergence events (subspeciation). Surprisingly, we find that the harsher conditions that typify temperate habitats (lower primary productivity, decreased rainfall and more variable and unpredictable temperatures) are positively correlated with greater subspecies richness in terrestrial mammals and birds. Thus, our findings indicate that intraspecific divergence is greater in regions with lower biodiversity, a pattern that is robust to both sampling variation and latitudinal biases in taxonomic knowledge. We discuss possible causal mechanisms for the link between environmental harshness and subspecies richness (faster rates of evolution, greater likelihood of range discontinuities and more opportunities for divergence) and conclude that this pattern supports recent indications that latitudinal gradients of diversity are maintained by simultaneously higher potentials for both speciation and extinction in temperate than tropical regions.**

*Keywords*: climate and evolution, comparative biology, latitudinal diversity gradients, raciation, subspeciation, subspecies richness

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## Introduction

Although temperate and tropical regions seem to support similar numbers of individuals in many major types of organisms (Enquist & Niklas 2001; Currie *et al.* 2004), species diversity tends to increase conspicuously around the tropics (Hillebrand 2004). This intriguing geographical pattern has been linked to latitudinal variation in biome area (Terborgh 1973), energy availability

(Currie *et al.* 2004), climatic conditions (Francis & Currie 2003), diversification rates (Weir & Schluter 2007), historical processes (Wiens & Donoghue 2004; Jetz & Fine 2012) and species interactions (Dobzhansky 1950). However, the relative importance and potential interactions between these putative causal drivers are still poorly understood (Wiens 2011).

Evolutionary processes are thought to be particularly important to the formation and maintenance of diversity gradients because speciation and extinction can alter the numbers of species within regions. Consistent with this view, multiple lines of evidence suggest that

Correspondence: Carlos A. Botero, Fax: 919 515 3355;
E-mail: cabotero@ncsu.edu

rates of net diversification (i.e. speciation minus extinction) are highest around the tropics (reviewed in Mittelbach *et al.* 2007), although exceptions exist (see Soria-Carrasco & Castresana 2012; Jansson *et al.* 2013). Whether this pattern is a product of latitudinal differences in speciation rates (e.g. Martin & McKay 2004; Cardillo *et al.* 2005; Jablonski *et al.* 2006; McKenna & Farrell 2006; Ricklefs 2006; Wright *et al.* 2006; Mittelbach *et al.* 2007; Phillimore *et al.* 2007; Eo *et al.* 2008; Martin & Tewksbury 2008), differential species turnover (Weir & Schluter 2007, 2008), or both, is a matter of debate. In other words, it is currently unclear whether tropical regions currently harbour greater biodiversity because they are especially fertile grounds for the formation of new species, that is, 'cradles of diversity', or because they are less likely to lose the species they already have, that is, 'museums of diversity' (Stebbins 1974).

Important methodological issues complicate the study of latitudinal variation in diversification rates. For example, each species occupies a range of latitudes and exists under a variety of ecological conditions. However, evolutionary studies often reduce the geographical location of each taxon to a single value: the centroid or mode latitude of its breeding distribution. Such simplifying approach can lead to potentially misleading characterizations of the conditions under which taxa exist. For example, globally distributed species may have the same centroids as taxa with narrow tropical ranges, and the centroids of species with disjoint or ring distributions may lie in localities where these species do not even occur. To avoid such obvious pitfalls, some studies have sampled only taxa with restricted latitudinal ranges (e.g. <20° in Phillimore *et al.* (2007)). Unfortunately, this conservative criterion can lead to a significant loss of valuable data and does not fully capture the striking variation in environmental conditions that is observed even at these smaller geographical scales (e.g. consider differences between Miami, FL, 25.8°N, and Portland, ME, 43.6°N; Rome, 41.8°N, and Oslo, 59.9°N; New Delhi, 28.7°N, and Bangalore, 12.9°N; or Dodoma, −6.2°N, and Pretoria, −25.8°N). In addition, latitudinal bandwidth limits may lead to biased results due to the preferential exclusion of temperate taxa, which tend to have larger breeding distributions than their tropical counterparts ('Rapoport's rule', see Stevens 1989). Other methodological issues that complicate the analysis of latitudinal variation in diversification processes relate to the limitations of current approaches for modelling character-state or geography-dependent diversification (e.g. Maddison *et al.* 2007; FitzJohn 2010; Goldberg *et al.* 2011). These models explicitly assume that (i) the relationship between character states and diversification rates is identical everywhere across the tree and (ii) that all of the variation in diversification

rates in the tree can be explained by the distribution of states in the character of interest. The assumption of process homogeneity is especially likely to be violated when analysing large phylogenetic data sets (see Alfaro *et al.* 2009; O'Meara 2012), as is typically the case in studies of global patterns of diversity. For example, in mammals and birds (the targets of this study), diversification rates show extreme variation across major clades, and representatives from fast-diversifying and slow-diversifying clades alike can be found in both tropical and temperate regions (Stadler 2011; Jetz *et al.* 2012). Similarly, given the many biotic and abiotic correlates of latitudinal diversity gradients (see Mittelbach *et al.* 2007), the assumption that latitude is the sole driver of diversification rates seems highly unsatisfactory.

To address these issues, we explore here the global patterns in evolutionary divergence with an explicitly mechanistic approach. We begin by acknowledging that latitude is a convenient proxy for variables that were historically difficult to measure. Thus, we assemble a broad data set of the environmental correlates of latitude (measured over entire species' distributions) and evaluate their effects directly on the process of evolutionary divergence. Second, given the limitations of current methods for estimating diversification rates on large collections of species, we explore instead the global patterns in recent divergence events within species (i.e. subspecies richness). The idea that subspecies represent instances of incipient speciation has a long history in evolutionary biology (Mayr 1940, 1942, 1982; O'Brien & Mayr 1991). In support of this view, molecular and empirical evidence indicates that avian subspecies tend to reflect populations with divergent evolutionary trajectories in terms of morphology and sexual signals (reviewed in Phillimore *et al.* 2007; Phillimore 2010), including clear differentiation into distinct phylogenetic clades in ca. 36% of subspecies (Phillimore & Owens 2006).

Our analyses include 2365 species of mammals and 6694 species of birds (missing species largely reflect the intentional exclusion of marine and domesticated lineages) and are informed by the most recent species-level molecular phylogenies available for each group (Bininda-Emonds *et al.* 2008; Jetz *et al.* 2012). In addition, they account for the potential effects of well-known correlates of subspecies richness, namely species' age, area of the breeding distributions, adult body size, island dwelling, habitat heterogeneity and historical exposure to glaciation (see Phillimore *et al.* 2007). We also consider the possibility that the formation of subspecies is less dependent on environmental parameters when species avoid environmental extremes through migration (birds) or hibernation (mammals) and address potential historical biases in the quality of

subspecies designations in tropical taxa (Gippoliti & Amori 2007; Tobias *et al.* 2008).

## Methods

### Data and data sources

All of our data have been deposited in Dryad (http://datadryad.org, doi:10.5061/dryad.sb175). Starting with all extant terrestrial species recognized in the most current taxonomies for mammals and birds, we excluded all domesticated species because their current distribution and subspecies richness are likely to be determined by anthropogenic influences. In addition, we excluded all members of the mammalian superfamily Muroidea because of 'the unrefined alpha level comprehension over vast geographical regions and the usual dearth of modern infraspecific studies to objectively delimit races and to vouch their distributions' (Musser & Carleton 2005). After removing species for which proper geographical, environmental or biometric data are not currently available, our final sample comprised 2365 of 5020 mammalian species (i.e. 47% of all extant species) and 6694 of 10063 extant avian species (i.e. 67% of all extant species). Subspecies richness ($\bar{x} \pm$ SE, mammals: 2.68 $\pm$ 0.08; birds: 3.15 $\pm$ 0.04) was obtained from Wilson & Reeder (2005) and Clements (2000) through Phillimore *et al.* (2007). Breeding distributions were obtained from the 2010 IUCN Red List of Threatened Species v. 2010.4. (available at: www.iucnredlist.org. Downloaded 17 Apr 2012), and BirdLife International (available at: www.birdlife.org. Downloaded 17 Apr 2012). Adult body mass data were obtained from the study by Jones *et al.* (2009) and Dunning (2007). Species' ages were approximated as the length of the corresponding terminal branches in the most recent time-calibrated molecular phylogenies including all extant species in each group (Bininda-Emonds *et al.* 2008; Jetz *et al.* 2012).

Each environmental variable (including the mean, variance and predictability of annual precipitation and temperature cycles) was first measured locally for every cell within a species' range and then averaged across the entire breeding distribution to produce a single mean value per species. Precipitation and temperature data were obtained from monthly global maps (0.5 × 0.5 degree cells) for the period of 1901–2009 from the CRU-TS 3.1 Climate Database (Mitchell & Jones 2005). Predictability was measured via Colwell's P (Colwell 1974), an information-theory-based index that captures variation in the onset, intensity and duration of periodic phenomena and ranges from 0 (completely unpredictable) to 1 (fully predictable). Net primary productivity data were obtained from Imhoff *et al.* (2004).

Hibernation data for mammals were obtained from Liow *et al.* (2009), Turbill *et al.* (2011) and Feldhamer *et al.* (2007) unless otherwise stated. Elevation data were obtained from the GTOPO30 data set (available at: lpdaac.usgs.gov/gtopo30/gtopo30.asp. Last accessed 17 April 2012), and mountains were identified based on elevation gradients with slopes equal or higher than 5 degrees (Fig. S1 in Supporting Information). In an effort to be consistent with prior work, we followed Phillimore *et al.* (2007) when quantifying island dwelling as a binary variable that indicates when 20% or more of the breeding range occurs on islands; habitat heterogeneity as the number of biomes covering at least 5% of a species breeding range (biome data from Olson *et al.* 2001); and historical exposure to glaciation as a binary variable distinguishing between species that had and had not exhibited more than 20% range overlap with areas glaciated in the last 21 000 years (glaciation coverage from Peltier 1993).

### Statistics

Severe multicollinearity problems (see Farrar & Glauber 1967) are common when multiple bioecological predictors are included in the same statistical model because these variables tend to be strongly correlated with each other. To prevent these problems, we reduced the initial set of continuous predictors to a smaller number of composite orthogonal variables via principal component analysis, PCA. Each variable in the original set was transformed, when required (following Osborne (2002)), and all variables were centred and scaled prior to PCA. For simplicity, we use throughout the PC scores from a single PCA that includes data from mammals and birds (Table 1).

We used Bayesian phylogenetic mixed models, BPMM, with quasi-Poisson error to explore the association between bioecological predictors and the number of subspecies per species. As in phylogenetic generalized least squares regression (PGLS) models (Butler & King 2004), this statistical technique accounts for the different levels of phylogenetic relatedness between species by estimating the variance–covariance structure of the model from an independently derived molecular phylogeny (Hadfield 2010). We began each analysis with a fully parameterized model and proceeded to simplify the list of predictors by excluding nonsignificant terms one at a time, removing interactions first when necessary. Nonsignificance was assessed from credible intervals, CI, that include zero, and MCMC $P$-values > 0.05 (Hadfield 2010). BPMM were implemented in R (sample code in Data S2 in Supporting Information) through the package MCMCglmm, using uninformative priors and uniformly low levels of belief

**Table 1** Principal components analyses of the continuous bioecological variables in our set of potential predictors of subspecies richness. Data from both mammals and birds are included. Standardized loadings of the main contributors to each component are highlighted in boldface

| Bio-ecological variable | Environmental harshness (PC1) | Geographical coverage (PC2) | Precipitation unpredictability (PC3) | Residual body size (PC4) | Uniqueness |
|---|---|---|---|---|---|
| ln (Annual variance in temperature) | **0.91** | 0.10 | 0.11 | 0.01 | 0.15 |
| Predictability of temperature cycles | **−0.89** | −0.02 | −0.12 | 0.00 | 0.19 |
| Sqrt (mean precipitation) | **−0.89** | 0.13 | 0.08 | −0.05 | 0.19 |
| (Mean temperature)$^2$ | **−0.80** | 0.20 | 0.06 | 0.02 | 0.31 |
| Net primary productivity | **−0.79** | 0.21 | 0.06 | −0.15 | 0.30 |
| Sqrt (Annual variance in precipitation) | **−0.75** | 0.27 | 0.35 | 0.00 | 0.24 |
| Habitat heterogeneity | **0.61** | 0.40 | 0.21 | −0.30 | 0.33 |
| ln (Area) | 0.29 | **0.78** | −0.18 | −0.35 | 0.14 |
| ln (Body size) | 0.08 | **0.51** | −0.38 | **0.75** | 0.02 |
| Predictability of precipitation cycles | −0.20 | −0.13 | **−0.86** | −0.34 | 0.09 |
| SS loadings | 4.76 | 1.23 | 1.12 | 0.92 | |
| % Cumulative variance explained | 0.48 | 0.60 | 0.71 | 0.80 | |

(Hadfield 2010). Model chains were run for 300 000 iterations with a burn-in of 10 000 iterations and thinning intervals of 50 iterations. To evaluate convergence, we assessed the mixing of MCMC chains visually (Hadfield 2010) and computed formal diagnostics suggested by Geweke (1992) and Heidelberger & Welch (1983) via the R-package 'coda' (Plummer *et al.* 2006). In the analysis of bird data, we accounted for phylogenetic uncertainty by performing analyses across 100 trees chosen at random from the set provided by Jetz *et al.* (2012). Thus, the statistics we report for bird models reflect averages across these 100 analyses and include the frequency of trees (*f*) for which MCMC *P*-values <0.05 (see Jetz *et al.* 2012).

## Results

PCA indicates that several ecological and morphological characters are strongly correlated in terrestrial mammals and birds (Table 1). The first component, which we will refer to as 'environmental harshness', captures differences in the level of exposure to drier, less productive environments, with colder, less predictable and more variable annual temperatures (higher scores = harsher environments). The second component, which we have termed 'geographical coverage', captures most of the remaining variation in breeding distribution (higher scores = larger areas) and suggests that species that occupy larger areas tend to have larger body sizes and to be present in a greater number of biome types. The third component is almost exclusively associated with the predictability of annual precipitation cycles (note the negative loading in Table 1), and the fourth component captures the remaining variation in body size (higher scores = larger species).

To clarify how these components may ultimately reflect latitudinal patterns, we explored their variation in temperate versus tropical species (Table 2). For this analysis, we classified latitudinal ranges as 'exclusively tropical' when a species' entire breeding distribution is contained within the tropics of Cancer and Capricorn (±23.4° latitude), 'exclusively temperate' when its entire breeding distribution is outside this region, and 'mixed distribution' otherwise. As expected, there is little latitudinal overlap on PC1: temperate mammals and birds occupy significantly drier, less productive environments, with colder, less predictable and more variable annual temperatures than their tropical counterparts (Fig. 1). Temperate species in both groups are also exposed to more unpredictable rainfall patterns, PC3, but the differences are less pronounced in this case than in PC1 (Fig. 1). Latitudinal variation in PC2 and PC4 differs between groups, with breeding distributions being larger in tropical mammals, but not in birds, and body sizes being larger in temperate mammals but smaller in temperate birds (Table 2).

Table 3 summarizes our findings on the potential bioecological correlates of subspecies richness. Our results indicate that intraspecific geographical divergence is influenced by similar factors in mammals and birds. In both groups, subspecies richness is greater in island dwellers as well as in species that have larger breeding distributions, smaller body size and have been historically exposed to glaciation (Fig. 2). Subspecies richness also increases with harsher environmental conditions, PC1 (Fig. 2), although this effect is not seen among birds that avoid climatic extremes through migration (see interaction term in Table 3, Fig 2E). Finally, subspecies richness peaks at intermediate rainfall unpredictability values in both mammals and birds (Fig. 2F).

**Table 2** Latitudinal differences in bioecological traits. Coefficients reflect the results of multinomial phylogenetic regression models with 'temperate' range as the reference category

| Bio-ecological variable | Mammals Posterior mean (95% CI) | Birds Posterior mean (95% CI) | $f^{\ddagger}$ |
|---|---|---|---|
| **Environmental harshness (PC1)** | | | |
| Intercept | 1.31 (0.93, 1.63)*** | 1.50 (1.35, 1.66)*** | 1.00 |
| Mixed | −0.17 (−0.19, −0.14)*** | −0.20 (−0.21, −0.18)*** | 1.00 |
| Tropical | −0.50 (−0.52, −0.47)*** | −0.49 (−0.51, −0.48)*** | 1.00 |
| **Geographical coverage (PC2)** | | | |
| Intercept | 0.02 (−0.93, 0.90) | 0.14 (−0.31, 0.59) | 0.00 |
| Mixed | 0.71 (0.63, 0.79)*** | 0.64 (0.59, 0.69)*** | 1.00 |
| Tropical | 0.25 (0.16, 0.32)*** | 0.04 (−0.01, 0.10) | 0.00 |
| **Precipitation unpredictability (PC3)** | | | |
| Intercept | −0.02 (−0.98, 0.99) | −0.60 (−1.16, −0.04)* | 0.76 |
| Mixed | 0.05 (−0.06, 0.14) | 0.46 (0.39, 0.53)*** | 1.00 |
| Tropical | −0.26 (−0.36, −0.16)*** | −0.08 (−0.15, −0.01)* | 0.76 |
| **Residual body size (PC4)** | | | |
| Intercept | 0.91 (−0.12, 2.03) | 0.72 (0.22, 1.22)** | 1.00 |
| Mixed | −0.41 (−0.49, −0.34)*** | −0.12 (−0.16, −0.07)*** | 1.00 |
| Tropical | −0.25 (−0.32, −0.17)*** | 0.11 (0.06, 0.16)*** | 1.00 |

$^{\ddagger}f$ = frequency of trees for which MCMC $P$-values < 0.05.
*p MCMC < 0.05.
**p MCMC < 0.01.
***p MCMC < 0.001.

Spatial sensitivity analyses indicate that these results are robust to variation in environmental conditions across species' ranges in both taxonomic groups (see Data S1 and Tables S1–S2 in Supporting Information).

Given historical biases in research effort and taxonomic sampling, it is possible that the number of subspecies per species is currently underestimated in some tropical birds (Tobias *et al.* 2008) and mammals (Gippoliti & Amori 2007). To evaluate the extent to which this potential bias may have influenced our findings, we replicated our analyses using only data from resident north-temperate species (as in Weir & Schluter 2008). As seen with the global data set, the effects of environmental harshness on subspecies richness are also significant among north-temperate birds and mammals (Fig. 3 and Table S3 in Supporting Information; BPMM for mammals: β for PC1 = 0.45, CI = 0.09 to 0.87, p MCMC = 0.023; BPMM for birds: β for PC1 = 0.53, CI = 0.16 to 0.90, p MCMC = 0.005, *f* = 1.00). However, we found that the effects of rainfall unpredictability are not significant in either of these groups, which is not surprising given that geographical variation in precipitation levels is relatively minor above the tropic of Cancer (see Fig. 2D in Jetz & Rubenstein 2011).

Because the robustness of subspecies characterization is particularly problematic in mammalian taxonomy (e.g. see Musser & Carleton 2005), we also replicated our analyses using only well-characterized mammalian groups at two different taxonomic levels. First, we analysed three of the best-known clades: Carnivora, Primates and Artiodactyla (N = 541 species). As in the analyses presented above, we found that environmental harshness exhibits a significant positive effect on subspecies richness when considering these three groups together and accounting for phylogenetic effects and other potential covariates of diversity (BPMM: β for ln(PC1) = 0.61, CI = 0.16 to 1.08, p MCMC = 0.007). Separate analyses for each clade indicates that environmental harshness has significant effects in Carnivora (Fig. 3C, BPMM: β for ln (PC1) = 1.05, CI = 0.38–1.70, p MCMC = 0.001), but not in Primates or Artiodactyla. This finding is not surprising given that Primates and Artiodactyla occur primarily at tropical latitudes where variation in the environmental contributors to PC1 is minimal. Perhaps more interesting is that we see no significant effects of rainfall unpredictability in this sample whether we analyse the three clades combined or separately. An additional sensitivity analysis on Sciuridae, the speciose, well-known and globally distributed family of squirrels (N = 193 species), confirms this result. Here too, environmental harshness is a
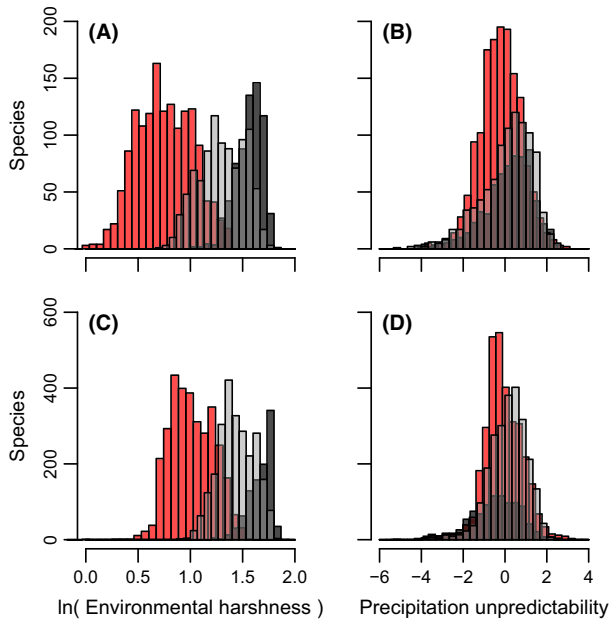
**Fig. 1** Distribution of species with exclusively tropical (red), exclusively temperate (black) and mixed (gray) breeding distributions along the axes of environmental harshness and precipitation unpredictability. Mammalian data are shown in (A) environmental harshness and (B) precipitation unpredictability. Avian data are shown in (C) environmental harshness and (D) precipitation unpredictability.

significant correlate of subspecies diversification (Fig. 3D, BPMM: β for ln(PC1) = 1.27, CI = 0.79–1.76, p MCMC < 0.001), but rainfall unpredictability is not.

## Discussion

Our findings are consistent with the hypothesis that physiology and ecology interact to promote latitudinal differences in the evolution of biological diversity (Janzen 1967). Importantly, the correlates of subspecies richness are remarkably similar in mammals and birds, and their effects are robust to accommodations for potential sampling biases and for biases related to incomplete knowledge of tropical taxonomy. Although it is clear from Primates and Artiodactyls that details may vary for particular groups (especially in predominantly tropical clades), our results indicate that at broader taxonomic scales, (i) there is a strong positive association between environmental harshness and the formation of subspecies and (ii) that this effect can generate some temperate–tropical differences in the evolution of intraspecific divergence.

Our key finding is that subspecies richness is greater when environmental conditions become more extreme as is increasingly the case in higher latitude habitats. Although this pattern is consistent with prior findings in New World mammals and birds (Weir & Schluter 2007), it is nevertheless surprising given that most indirect evidence suggests that the tropics, not the temperate regions of the world, are hotbeds for biological diversity (Mittelbach *et al.* 2007). Furthermore, greater subspecies richness in exclusively temperate taxa could be considered suspicious because the historically better taxonomic knowledge of temperate regions could have

**Table 3** Summary of results for Bayesian phylogenetic mixed models of subspecies richness in extant terrestrial mammals (excluding Muroidea) and birds

| Parameter | Mammals[†]<br>Posterior mean (95% CI) | Birds[†]<br>Posterior mean (95% CI) | $f^{‡}$ |
|---|---|---|---|
| Intercept | −1.16 (−2.66, 0.33) | −1.27 (−1.92, 0.63) *** | 1.00 |
| Dissected by mountains | 0.89 (0.70, 1.08)*** | 0.37 (0.29, 0.44)*** | 1.00 |
| Environmental shielding[§] | N.S. | 1.05 (0.35, 1.75)** | 1.00 |
| Glaciation | N.S. | 0.17 (0.00, 0.34)* | 0.60 |
| Island dwelling | 0.33 (0.01, 0.01)* | 0.66 (0.55, 0.77)*** | 1.00 |
| ln(species age) | N.S. | N.S. | 0.00 |
| ln(environmental harshness, PC1) | 1.15 (0.79, 1.52)*** | 0.74 (0.55, 0.92)*** | 1.00 |
| Geographical coverage, PC2 | 0.84 (0.71, 0.98)*** | 0.67 (0.59, 0.74)*** | 1.00 |
| Precipitation unpredictability, PC3 | −0.24 (−0.36, −0.12)*** | −0.04 (−0.10, 0.01) | 0.00 |
| PC3$^2$ | −0.06 (−0.11, −0.01)* | −0.03 (−0.06, −0.01)* | 1.00 |
| Residual body size, PC4 | −0.17 (−0.31, −0.03)* | −0.46 (−0.54, −0.38)*** | 1.00 |
| ln(environmental harshness)* Environmental shielding | N.S. | −0.88 (−1.35, −0.42)*** | 1.00 |
| Precipitation unpredictability* Environmental shielding | N.S. | N.S. | 0.00 |

[†]N.S, not significant.
[‡]$f$ = frequency of trees for which MCMC *P*-values < 0.05.
[§]Hibernation in mammals, migration in birds.
*p MCMC < 0.05.
**p MCMC < 0.01.
***p MCMC < 0.001.
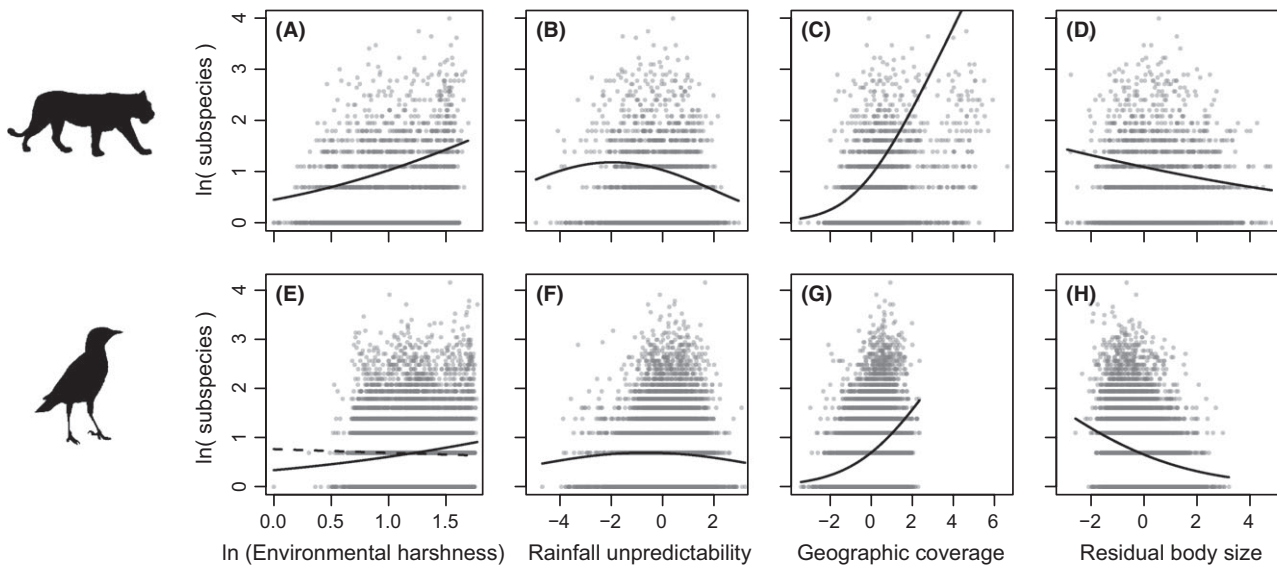
**Fig. 2** Bioecological correlates of subspecies richness in extant terrestrial mammals and birds. Individual species are depicted as points and lines reflect fits from phylogenetically informed Poisson regression models (computed at the average value for each of the other predictors in the model). Variables on the x-axes were derived via principal components analysis. Higher scores for environmental harshness (A, E) reflect increased exposure to drier, less productive environments, with colder, less predictable and more variable temperatures. Higher rainfall unpredictability scores (B, F) imply exposure to cycles with greater interyear variation in duration, onset and extent of the rainy season. Higher scores for geographical coverage (C, G), reflect larger, more heterogeneous breeding distributions and larger body sizes. Residual body size scores (D, H) reflect the remaining variation in body size. Panel E includes regression lines fitted for migrants (dashed line) and nonmigrants (solid line). Because ln(0) is not defined, ln (environmental harshness) was computed as ln(PC1(x) - min(PC1) + 1) following Osborne(2002).
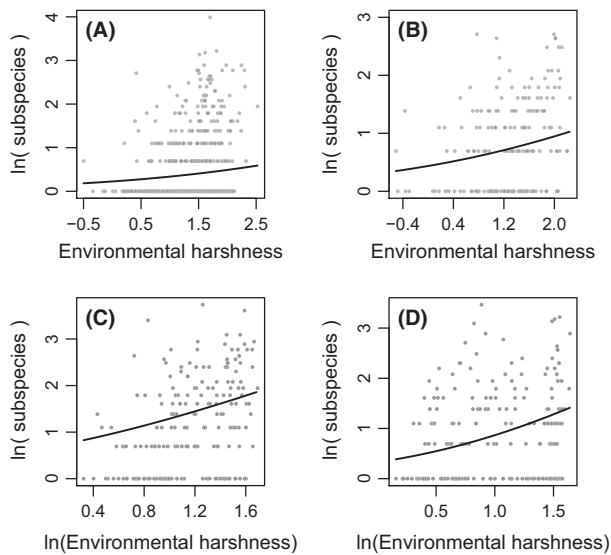


**Fig. 3** Variation in subspecies richness as a function of environmental harshness in (A) north-temperate mammals, (B) north-temperate birds, (C) Carnivora and (D) Sciuridae. Individual species are depicted as points and lines reflect fits from phylogenetically informed Poisson regression models that account for other potential covariates of subspecies richness (computed at the average value for each of the other predictors in the model).

increased our chances of recognizing interpopulation differences (and of labelling these populations as different subspecies), artificially resulting in the same geographical pattern. Regarding these concerns, we note that (i) the positive effect of environmental harshness on subspecies richness is strong even if only north-temperate taxa are included in the analysis (i.e. the region of the world we presumably know best) and that (ii) the same result is obtained when only particularly well-studied and globally distributed groups such as Carnivora or Sciuridae are considered. Thus, the higher propensity for speciation in temperate regions could be reconciled with the reality of higher tropical diversity by considering that net diversity is the product of both speciation and extinction and that the gradients we see today may be generated by higher species turnover (i.e. simultaneously high speciation and extinction rates) in temperate than tropical regions (Schluter & Weir 2007; Weir & Schluter 2007, 2008). This possibility appears to be well supported by the abundant anecdotal evidence linking environmental harshness with higher probabilities of extinction (e.g. see Hardie & Hutchings 2010).

We see at least three possible explanations for the positive association between environmental harshness and subspecies richness. First, the stronger natural and/or sexual selection typically associated with harsher envi-

ronmental conditions (see Botero *et al.* 2009) is likely to translate into faster rates of evolution (see Estes & Arnold 2007). Thus, other things being equal, populations in more extreme environments could conceivably diverge more quickly and may therefore be more likely to evolve into different subspecies or reproductively isolated lineages than those exposed to milder conditions. Alternatively, more extreme environments could simply provide more frequent opportunities to diverge in allopatry (Hua & Wiens 2013) because they are more likely to exhibit the type of extreme weather events that can result in local extinction and range discontinuities (see Hawkins *et al.* 2006; Jablonski *et al.* 2006; Schluter & Weir 2007). A related possibility is that more extreme environments offer more opportunities for diversification, for example through unexploited niches, because communities are less likely to achieve or maintain equilibrium under high rates of local extinction (see Rabosky 2009). The potentially opportunistic nature of evolutionary divergence is supported by the fact that subspecies richness did not simply increase with species age in any of our models (see Rabosky 2009).

At a global scale, our results indicate that characterizing the association between latitude and subspecies richness as a unidirectional gradient is overly simplistic and potentially misleading (see also Jetz *et al.* 2012 for a similar point of view). Specifically, different correlates of latitude appear to influence intraspecific divergence in different ways, a detail that can be overlooked when we refer to the collection of latitudinal effects as a single latitudinal gradient. For example, latitudinal patterns in body size and breeding distribution suggest lower temperate than tropical subspecies richness in mammals, whereas variation in environmental harshness suggest the opposite trend. The interaction between different environmental correlates of latitude could therefore potentially explain why studies that include different species and/or involve different regions of Earth (where the relative importance of these environmental parameters may differ) have arrived at different conclusions regarding the role of latitude on speciation rates (see Jablonski *et al.* 2006; McKenna & Farrell 2006; Wright *et al.* 2006; Mittelbach *et al.* 2007; Weir & Schluter 2007, 2008; Brochmann & Brysting 2008; Tobias *et al.* 2008).

We conclude that several key environmental correlates of latitude predict the evolution of intraspecific divergence in birds and mammals and that they are likely to explain some geographical differences in the potential for speciation. Similarly, we conclude that global patterns of subspecies richness are consistent with the notion that temperate regions are currently important producers of biological diversity (Schluter & Weir 2007; Weir & Schluter 2007, 2008) and suggest that

future studies may benefit from a greater appreciation for the potential role of extinction and species turnover on the formation and maintenance of global patterns of diversity.

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## References

Alfaro ME, Santini F, Brock C *et al.* (2009) Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences*, **106**, 13410–13414.

Bininda-Emonds ORP, Cardillo M, Jones KE *et al.* (2008) The delayed rise of present-day mammals. *Nature*, **446**, 507–512.

Botero CA, Boogert NJ, Vehrencamp SL, Lovette IJ (2009) Climatic patterns predict the elaboration of song displays in mockingbirds. *Current Biology*, **19**, 1151–1155.

Brochmann C, Brysting AK (2008) The Arctic - an evolutionary freezer? *Plant Ecology & Diversity*, **1**, 181–195.

Butler MA, King AA (2004) Phylogenetic comparative analysis: a modeling approach for adaptive evolution. *American Naturalist*, **164**, 683–695.

Cardillo M, Orme CDL, Owens IPF (2005) Testing for latitudinal bias in diversification rates: an example using New World birds. *Ecology*, **86**, 2278–2287.

Clements JF (2000) *Birds of the World: A Checklist*. Ibis Vista, California.

Colwell RK (1974) Predictability, constancy, and contingency of periodic phenomena. *Ecology*, **55**, 1148–1153.

Currie DJ, Mittelbach GG, Cornell HV *et al.* (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

Dobzhansky T (1950) Evolution in the tropics. *American Scientist*, **38**, 209–221.

Dunning JB (2007) *CRC Handbook of Avian Body Masses*, 2nd edn. CRC Press, Boca Raton, Florida.

Enquist BJ, Niklas KJ (2001) Invariant scaling relations across tree-dominated communities. *Nature*, **410**, 655–660.

Eo SH, Wares JP, Carroll JP (2008) Population divergence in plant species reflects latitudinal biodiversity gradients. *Biology Letters*, **4**, 382–384.

Estes S, Arnold SJ (2007) Resolving the paradox of stasis: models with stabilizing selection explain evolutionary divergence on all timescales. *American Naturalist*, **169**, 227–244.

Farrar DE, Glauber RR (1967) Multicollinearity in regression analysis: the problem revisited. *The Review of Economics and Statistics*, **49**, 92–107.

Feldhamer GA, Drickamer LC, Vessey SH, Merritt JF, Krajewski C (2007) *Mammalogy: Adaptation, Diversity, and Ecology*, 3rd edn. John Hopkins Press, Baltimore, Maryland.

FitzJohn RG (2010) Quantitative traits and diversification. *Systematic Biology*, **59**, 619–633.

Francis AP, Currie DJ (2003) A globally consistent richness-climate relationship for angiosperms. *American Naturalist*, **161**, 523–536.

Geweke J (1992) Evaluating the accuracy of sampling-based approaches to calculating posterior moments. In: *Bayesian Statistics 4* (eds Bernado J, Berger J, Dawid A & Smith A). Clarendon Press, Oxford, UK.

Gippoliti S, Amori G (2007) The problem of subspecies and biased taxonomy in conservation lists: the case of mammals. *Folia Zoologica*, **56**, 113–117.

Goldberg EE, Lancaster LT, Ree RH (2011) Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. *Systematic Biology*, **60**, 451–465.

Hadfield JD (2010) MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software*, **33**, 1–22.

Hardie DC, Hutchings JA (2010) Evolutionary ecology at the extremes of species' ranges. *Environmental Reviews*, **18**, 1–20.

Hawkins BA, Diniz-Filho JAF, Jaramillo CA, Soeller SA (2006) Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of new World birds. *Journal of Biogeography*, **33**, 770–780.

Heidelberger P, Welch P (1983) Simulation run length control in the presence of an initial transient. *Operations Research*, **31**, 1109–1144.

Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *American Naturalist*, **163**, 192–211.

Hua X, Wiens JJ (2013) How does climate influence speciation? *American Naturalist*, **182**, 1–12.

Imhoff ML, Bounoua L, Ricketts T et al. (2004) Global patterns in human consumption of net primary production. *Nature*, **429**, 870–873.

Jablonski D, Roy K, Valentine JW (2006) Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science*, **314**, 102–106.

Jansson R, Rodríguez-Castañeda G, Harding LE (2013) What can multiple phylogenies say about say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution*, **67**, 1741–1755.

Janzen DH (1967) Why mountain passes are higher in the tropics. *American Naturalist*, **101**, 233–249.

Jetz W, Fine PVA (2012) Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology*, **10**, e1001292.

Jetz W, Rubenstein DR (2011) Environmental uncertainty and the global biogeography of cooperative breeding in birds. *Current Biology*, **21**, 72–78.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. *Nature*, **491**, 444–448.

Jones KE, Bielby J, Cardillo M et al. (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology*, **90**, 2648.

Liow LH, Fortelius M, Lintulaakso K, Mannila H, Stenseth NC (2009) Lower extinction risk in sleep-or-hide mammals. *American Naturalist*, **173**, 264–272.

Maddison WP, Midford PE, Otto SP (2007) Estimating a binary character's effect on speciation and extinction. *Systematic Biology*, **56**, 701–710.

Martin PR, McKay JK (2004) Latitudinal variation in genetic divergence of populations and the potential for future speciation. *Evolution*, **58**, 938–945.

Martin PR, Tewksbury JJ (2008) Latitudinal variation in subspecific diversification of birds. *Evolution*, **62**, 2775–2788.

Mayr E (1940) Speciation phenomena in birds. *American Naturalist*, **74**, 249–278.

Mayr E(1942) *Systematics and the Origin of Species from the Viewpoint of a Zoologist*. Columbia University Press, New York.

Mayr E (1982) *The Growth of Biological Thought: Diversity, Evolution, and Inheritance* . Belknap Press of Harvard University Press, Cambridge, Massachusetts.

McKenna DD, Farrell BD (2006) Tropical forests are both evolutionary cradles and museums of leaf beetle diversity. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 10947–10951.

Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *International Journal of Climatology*, **25**, 693–712.

Mittelbach GG, Schemske DW, Cornell HV et al. (2007) Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters*, **10**, 315–331.

Musser GG, Carleton MD (2005) Superfamily Muroidea. In: *Mammal Species of the World. A Taxonomic and Geographic Reference*, 3rd edn. (eds Wilson DE & Reeder DM), pp. 894–1531. Johns Hopkins University Press, Baltimore, Maryland.

O'Brien SJ, Mayr E (1991) Bureaucratic mischief: recognizing endangered species and subspecies. *Science*, **251**, 1187–1188.

Olson DM, Dinerstein E, Wikramanayake ED et al. (2001) Terrestrial ecoregions of the worlds: a new map of life on Earth. *BioScience*, **51**, 933–938.

O'Meara BC (2012) Evolutionary inferences from phylogenies: a review of methods. *Annual Review of Ecology, Evolution, and Systematics*, **43**, 267–285.

Osborne J (2002) Notes on the use of data transformations. Practical Assessment, Research and Evaluation http://pareonline.net 8 (6).

Peltier WR(1993) Time dependent topography through the glacial cycle. IGBP PAGES/World Data Center-A for Paleoclimatology Data Contribution Series 93-015, NOAA/NGDC Paleoclimatology Program. Available at http://geochange.er.usgs.gov/data/sea_level/Core/raw/peltier/. Boulder, CO.

Phillimore AB (2010) Subspecies origination and extinction in birds. *Ornithological Monographs*, **67**, 42–53.

Phillimore AB, Owens IPF (2006) Are subspecies useful in evolutionary and conservation biology? *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1049–1053.

Phillimore AB, Orme CDL, Davies RG et al. (2007) Biogeographical basis of recent phenotypic divergence among birds: a global study of subspecies richness. *Evolution*, **61**, 942–957.

Plummer M, Best N, Cowles K, Vines K (2006) CODA: convergence diagnosis and output analysis for MCMC. *R News*, **6**, 7–11.

Rabosky DL (2009) Ecological limits and diversification rate: alternative paradigms to explain the variation in species richness among clades and regions. *Ecology Letters*, **12**, 735–743.

Ricklefs RE (2006) Global variation in the diversification rate of passerine birds. *Ecology*, **87**, 2468–2478.

Schluter D, Weir J (2007) Explaining latitudinal diversity gradients - response. *Science*, **317**, 452–453.

Soria-Carrasco V, Castresana J (2012) Diversification rates and the latitudinal gradient of diversity in mammals. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 4148–4155.

Stadler T (2011) Inferring speciation and extinction processes from extant species data. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 16145–16146.

Stebbins GL (1974) *Flowering Plants: Evolution Above the Species Level*. The Belknap Press of Harvard Univ. Press, Cambridge, Massachusetts.

Stevens GC (1989) The latitudinal gradient in geographical range: how so many species coexist in the tropics. *American Naturalist*, **133**, 240–256.

Terborgh J (1973) On the notion of favorableness in plant ecology. *American Naturalist*, **107**, 481–501.

Tobias JA, Bates JM, Hackett SJ, Seddon N (2008) Comment on "The latitudinal gradient in recent speciation and extinction rates of birds and mammals". *Science (New York, N.Y.)*, **319**, 901.

Turbill C, Bieber C, Ruf T (2011) Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 3355–3363.

Weir JT, Schluter D (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, **315**, 1574–1576.

Weir JT, Schluter D (2008) Response to comment on the latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, **319**, 901.

Wiens JJ (2011) The causes of species richness patterns across space, time, and clades and the role of ecological limits. *Quarterly Review of Biology*, **86**, 75–96.

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, **19**, 639–644.

Wilson DE, Reeder DM (2005) *Mammal Species of the World. A Taxonomic and Geographic Reference* (3rd edn.), p. 2142. Johns Hopkins University Press, Baltimore, Maryland.

Wright S, Keeling J, Gillman L (2006) The road from Santa Rosalia: a faster tempo of evolution in tropical climates. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 7718–7722.

# Data accessibility

Data Archival Location: Dryad (http://datadryad.org), doi:10.5061/dryad.sb175

# Supporting information

Additional supporting information may be found in the online version of this article.

**Data S1** Spatial sensitivity analysis.

**Data S2** Sample code for Bayesian Phylogenetic Mixed Models (BPMM) in R.

**Table S1** Principal components analyses of continuous bio-ecological variables in the spatial sensitivity analysis.

**Table S2** Summary of results for the Bayesian Phylogenetic Mixed Models of subspecies richness in the spatial sensitivity analysis.

**Table S3** Summary of results for the Bayesian Phylogenetic Mixed Models of subspecies richness in north temperate mammals and birds.

**Fig. S1** Elevation gradients of the world and three representative examples of species whose breeding ranges are dissected by mountains.