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Hawkins, B A
Diniz, JAF
Soeller, S A

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Water links the historical and contemporary components of the Australian bird diversity gradient

Bradford A. Hawkins[1]*, José Alexandre Felizola Diniz-Filho[2] and Stephen A. Soeller[3]

[1]*Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, USA, [2]Departamento de Biologia Geral, ICB, Universidade Federal de Goiás, Goiânia, and Departamento de Biologia, MCAS/PROPE, Universidade Católica de Goiás, Goiânia, GO, Brazil and [3]Network and Academic Computing Services, University of California, Irvine, CA, USA*

ABSTRACT

Aim To document the geographical structure of the historical signal in the continental species richness gradient of birds and evaluate the influences of contemporary and historical climatic conditions on the generation and maintenance of the richness pattern.

Location Australia.

Methods We used range maps of breeding birds to generate the spatial pattern of species richness at four grain sizes, and two molecular phylogenies to measure the level of evolutionary development of avifaunas at each grain size. We then used simple correlation and path analysis to generate a statistical model of species richness using environmental predictor variables and compared the spatial patterns of richness and mean evolutionary development to identify possible environmental links between richness and net diversification rates across the continent.

Results The contemporary richness pattern is well explained statistically by actual evapotranspiration (a measure of water–energy balance), operating both directly and indirectly through plant production, and this is robust to the spatial resolution of the analysis. Further, species richness and the mean level of evolutionary development of faunas show a strong spatial correspondence, such that dry areas support both fewer species and species from more highly derived families, whereas wet areas support more species of both basal and derived families. The evolutionary pattern conforms to a similar pattern known for plants and is probably explained by the increase in aridity in western and central Australia arising in the Miocene.

Main conclusion The contemporary bird richness gradient contains a historical signal and reflects the effects of both current levels of water availability as well as changes in rainfall patterns extending over evolutionary time. The historical signal persists even in the absence of obvious hard barriers to dispersal.

Keywords

Climate change, diversification rates, diversity gradients, mean root distance, Normalized Difference Vegetation Index, species richness, water–energy balance.

*Correspondence: Bradford A. Hawkins, Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA.
E-mail: bhawkins@uci.edu

INTRODUCTION

The global pattern of bird species richness is known to be strongly associated with actual evapotranspiration (AET) (Hawkins *et al.*, 2003a), a composite climatic variable describing the simultaneous availability of energy and water (Stephenson, 1990). In cold parts of the world, such as polar and boreal zones, energy represents the limiting component of the interaction, whereas in the tropics, subtropics and warm temperate areas, AET is determined by rainfall. This suggests that diversity at high latitudes is primarily constrained by temperature, whereas in high-energy, low latitudes, bird species richness responds primarily to rainfall patterns. Although a number of mechanisms have been proposed to explain associations between climate and richness, evaluation of the supporting evidence has been inconclusive (Currie *et al.*,

2004). Even so, statistical associations between species richness and contemporary climate beg the question of what causes species to be added to or removed from the global pool over evolutionary time, which clearly contributes to existing broad-scale richness gradients (Jablonski, 1991; McGlone, 1996; Cardillo, 1999; Ricklefs, 2004).

Discussions of the importance of factors operating in ecological and evolutionary time are sometimes based on the view that they represent alternative explanations (Currie & Paquin, 1987; Latham & Ricklefs, 1993; Kerr & Currie, 1999; Francis & Currie, 2003; Qian & Ricklefs, 2004), although the influence of climate change on extinction rates is universally appreciated (see e.g. McGlone, 1996; Dynesius & Jansson, 2000; Thomas *et al.*, 2004). But, most workers would probably agree that both history and contemporary climate influence richness, and a focal problem is to determine how the past and present are linked, and what specific aspects of history have the strongest influences.

In this paper, we examine how the contemporary species richness pattern and one of its evolutionary components covary in space. We expect covariation based on two related suppositions. First, a combination of past and current climates is the primary driver of diversity, and the same elements of climate that currently constrain richness have also influenced historical patterns of richness, because the latter is the signal of how the patterns have responded to climate change operating through evolutionary time. This builds on long-standing ideas that diversity is high in tropical areas because climates there have been warm for a long time or influence diversification by increasing speciation rates and decreasing extinction rates (Pianka, 1966; Jablonski, 1991; Rohde, 1992; Cardillo, 1999). The second supposition is that climate (both past and present) influences animal diversity through both direct effects (operating through the physiological tolerances of animals due to heat/cold stress and water availability; an effect encapsulated in the 'ambient energy' hypothesis) and indirectly through plants (which supply a wide range of services to animals, including a resource base (the 'productivity' hypothesis), nesting sites, protection from predators, etc.) (Hawkins *et al.*, 2003a; Willig *et al.*, 2003). Because it is well established that bird diversity is influenced by vegetation structure (MacArthur, 1961), and the biological and ecological traits of bird families are conserved during evolution (Bennett & Owens, 2002), bird speciation and extinction patterns and hence species richness might also be expected to track long-term changes in vegetation.

We examine these suppositions by first generating an environmental model to explain the contemporary richness pattern of Australian birds. This identifies the probable factors acting on the currently existing gradient. We then test for a historical signal in the richness gradient using the method of Kerr & Currie (1999), by generating a measure of the degree of evolutionary development of the avifauna across Australia using two molecular phylogenies. In the absence of direct estimates of speciation and extinction rates, which are difficult

to obtain, comparing the contemporary pattern with its phylogenetic structure may give insights into the likely processes that have also influenced diversification patterns across the continent. If the richness pattern and pattern of evolutionary development covary, we can conclude that similar factors may explain both the past and present.

METHODS

Bird species richness and MRD

Presumed breeding ranges (whether seasonal or year-round) for 527 native Australian bird species (Simpson & Day, 1984) were digitized into ArcGIS 8.3 and rasterized at four grain sizes using nested grid systems of 27.5×27.5, 55×55, 110×110, and 220×220 km (equivalent to 0.25°, 0.5°, 1° and 2° of latitude) Species richness was calculated directly from the rasters. Root distance for each species was obtained first using Sibley & Ahlquist's (1990) comprehensive phylogenetic tree for the entire bird clade, based on DNA–DNA hybridization patterns. Each species was assigned to a family using the classification provided by Sibley & Monroe (1990), and the root distance of the bird's family was calculated. Root distance represents the number of nodes separating a species' family from the base of the tree, and the mean root distance (MRD) of all bird species resident in each cell is used as a measure of the level of evolutionary development of the local avifauna (Kerr & Currie, 1999). Thus, cells with high values support species that are, on average, from more highly derived families.

Phylogenetic trees for birds based on DNA hybridization are very controversial (e.g. Cracraft, 1987; Mindell, 1992) but Sibley & Ahlquist (1990) is the only tree of which we are aware that includes all bird families. However, a tree for the passerines based on DNA sequence data has recently become available (Barker *et al.*, 2004). To examine the sensitivity of the analysis to tree topology, we merged the non-passerine part of the tree from Sibley & Ahlquist (1990) with the passerine tree of Barker *et al.* (2004) and recalculated MRDs based on this hybrid tree. As far as we know there is no sequence-based tree for non-passerines available.

Environmental predictors

Correlates of the contemporary richness gradient were examined using five environmental variables known to be associated with animal species richness gradients (e.g. Rahbek & Graves, 2001; Hawkins *et al.*, 2003a,b; Hurlbert & Haskell, 2003), generated using ArcGIS software. Global raster data files were downloaded from Internet sites, subsets of which were extracted for Australia, and the data for each variable were further processed using consistent procedures at each grain size:

Normalized Difference Vegetation Index (NDVI) (ftp://crsa.bu.edu/pub/rmyneni/myneniproducts/datasets/AVHRR_DATASETS/PATHFINDER/VERSION3_DATA/NDVI/): This is a measure of 'greenness' being widely used to estimate plant

biomass or net primary production (Hurlbert & Haskell, 2003 and references therein). Nineteen annual raster data sets covering the years 1982–2000 were averaged within each cell.

Landcover diversity (http://edcdaac.usgs.gov/glcc/globe_int. html): Global landcover characteristics, mapped at 1-km resolution, were used. The landcover value represents the number of distinct landcover types within the cell.

Elevation range (http://lpdaac.usgs.gov/gtopo30/gtopo30.asp): GTOPO30 digital elevation model (DEM) data with a horizontal grid spacing of 30 arc-seconds were used. A value representing the range between the minimum and the maximum elevation within each cell was calculated.

Annual potential evapotranspiration (PET, Priestley–Taylor formula) and annual AET (Thornthwaite's) (http://www. grid.unep.ch/data/grid/gnv183.php): Raster data, initially comprising 0.5° cells, were subsampled at 0.2°. The maximum value for each variable within each cell was used.

Processing was performed at all grain sizes using a Lambert azimuthal equal-area projection. At each grain size, coastal cells were excluded from the analysis if they contained < 50% of the land mass of inland cells.

Statistical analyses

Species richness and environmental data collected in a grid system display spatial autocorrelation, reflecting spatial non-independence of the data due to the proximity of grid cells. This generates bias in the type I error of statistical tests due to overestimation of degrees of freedom. All significance tests were performed using a reduced degrees of freedom (v^*), based on the geographically effective sample size (Griffith, 2003). v^* was calculated using MODTTEST (available from http://www. bio.umontreal.ca/legendre/), modified to allow larger sample sizes, and based on Moran's I spatial autocorrelation coefficients calculated for each variable using 18 geographical distance classes across the continent.

Analyses consisted of simple correlation and path analysis. Path coefficients were obtained iteratively using the maximum Wishart likelihood method based on the correlation matrix among variables, implemented in the RAMONA routine of SYSTAT 10.0 (Browne & Mels, 2000) and tested using v^* degrees of freedom ($\cong 11$) estimated by MODTTEST for pairwise correlations among variables.

Analyses were conducted at all four grain sizes, but because results were very similar (see Table 1) we focus on those at 110×110 km. In addition, focusing the analysis on a larger grain reduces errors in the richness data due to false positives, which are inherent to estimating species richness using range maps and likely to be very common at the smaller grain sizes.

Mean root distances may be sensitive to richness in each grid cell because, as richness increases, the mean score must shift towards the overall mean of root distance of all species in the continent. In addition, there must be an intrinsic correlation between the two variables, as richness is the denominator of MRD (Brett, 2004). So, the correlation

Table 1 Correlation coefficients for environmental variables and bird species richness at four grain (cell) sizes

Variable	Grain size (km)			
	27.5×27.5	55×55	110×110	220×220
Actual evapotranspiration	0.765**	0.771**	0.782**	0.788**
Normalized Difference Vegetation Index	0.766**	0.775**	0.780**	0.790**
Landcover diversity	0.342**	0.462**	0.578*	0.616*
Range in elevation	0.452**	0.479**	0.519**	0.508*
Potential evapotranspiration	0.121	0.134	0.126	0.105
Number of cells	10,020	2515	627	157

Significance tests (*$P < 0.05$, **$P < 0.01$) used geographically effective degrees of freedom (v^*), which ranged from 10 to 34. Also given is the number of cells analysed at each grain size.

coefficient for richness and MRD under the null hypothesis of no correlation may be greater than zero. To avoid these problems, two different randomization procedures were used. The first procedure allowed us to obtain the expected MRD in each cell, by sampling without replacement the species in the overall species pool according to the observed species richness. This procedure creates a statistical distribution of null MRDs for each cell, and a normalized Z-score for each cell was calculated by subtracting observed and expected MRDs, divided by its standard error. Thus, Z-scores higher than 1.96 indicate that there is a 95% chance that the MRD in the cell is higher than would be expected if species found there were a random sample of the overall species pool in Australia. The second randomization was done to correct for any intrinsic correlation between richness and MRD, by randomizing the sum of RD values in each cell and recalculating MRD before computing the correlation. Thus, this procedure allows us to test the significance of the observed correlation after incorporating the null distribution of correlation coefficients due to the fact that richness is in the denominator of MRD. In both procedures, 10,000 randomizations were used.

RESULTS AND DISCUSSION

The geographical pattern of species richness is similar to that found for many plant and animal taxonomic groups in Australia, with richness being highest on the east coast and lowest in the central and western deserts (Fig. 1a). Among the five environmental variables, water–energy balance (measured by AET) and plant biomass (measured by the NDVI) were the strongest predictors of richness at all grain sizes (Table 1), although measures of environmental heterogeneity appear to be relatively stronger secondary predictors at larger grains. However, positive collinearity between AET, NDVI and landcover diversity is present in the data, because plant production and richness are themselves strongly dependent on water and energy
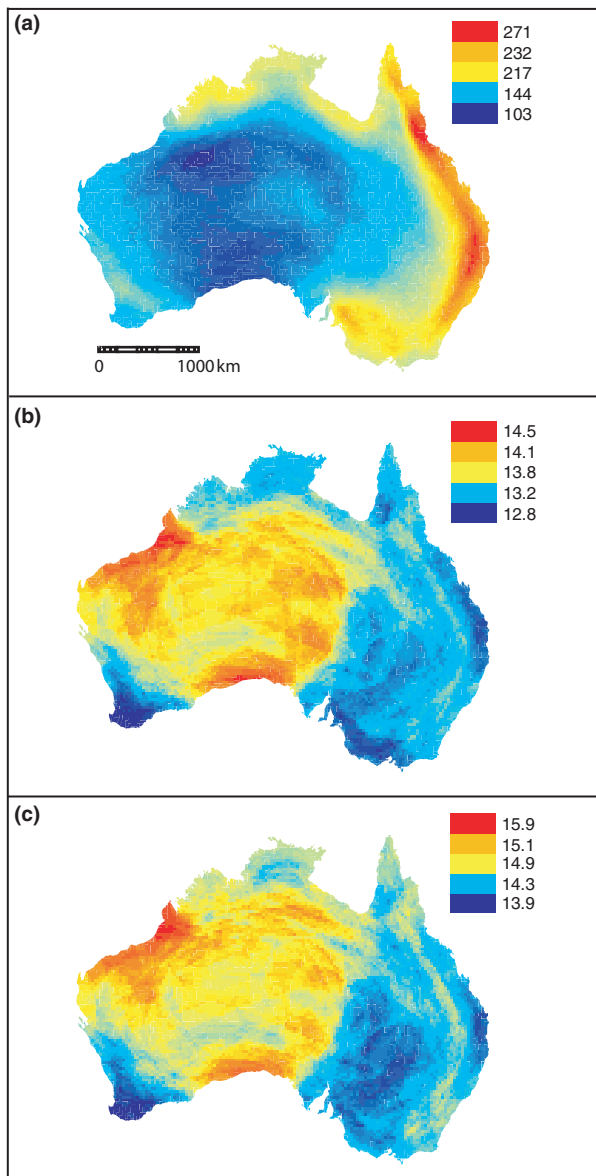
(a)

(b)

(c)

Figure 1 Geographical patterns of (a) species richness, (b) mean root distance resolved at the family level for Australian birds at 27.5 × 27.5 km grain size, based on the tree of Sibley & Ahlquist (1990), and (c) mean root distance based on a hybrid tree in which the passerine section of Sibley & Ahlquist's tree was replaced with the tree of Barker *et al.* (2004). Species richness is highest along the east coast and lowest in the central and western deserts. Further, based on both trees the deserts are characterized by bird faunas from more highly derived families, whereas in wetter parts of Australia the birds in each cell are on average from more basal families.

at large extents. To explore the relationships between bird richness, plants and climate, we generated two path models assuming that AET influences bird richness both directly and indirectly through its effects on plant productivity and landcover diversity. The first model (Fig. 2a) included both NDVI and landcover, with both being moderated by water–
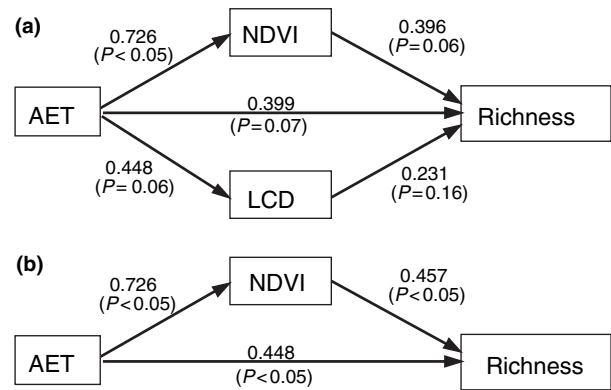
(a)

(b)

Figure 2 Path models for testing relationships between water–energy balance (actual evapotranspiration, AET), plant production (Normalized Difference Vegetation Index, NDVI), landcover diversity (LCD), and bird species richness, using data resolved at 110 × 110 km grain size. (a) Model assuming that bird richness is driven by both plant production and landcover diversity, both of which are driven by climate. Climate is also assumed to have direct effects on birds through heat and water stress. (b) Version of model in which landcover diversity has been removed. Path coefficients for both models were tested for significance taking into account spatial autocorrelation by using $v^\star = 11$. The model including landcover explains 74.6%, whereas the simpler model explains 70.7% of the variance in richness.

energy balance. However, using a very low number of degrees of freedom suggested by Duttileul's method, only one of the path coefficients was significant at the 5% level, although direct and indirect effects of AET were all marginally significant ($P = 0.06$). The non-significant link between landcover and richness also indicates that the simple correlation between landcover diversity and richness (Table 1) is largely due to covariation with other variables, and that it can be deleted from the model. After removing landcover all path coefficients become significant (Fig. 2b), further indicating that the cause-and-effect relationships hypothesized by the model including landcover are weak. So, we accept the simpler model as being stronger. The coefficients in this model indicate that climate and plant production have equally strong direct effects on birds, but the total effect of water–energy is strongest (total path coefficient = 0.782), because of its influence on plants. Thus, the contemporary species richness gradient of Australian birds is well described statistically by current temperature and rainfall patterns, consistent with a previous intercontinental analysis (Hawkins *et al.*, 2003a). Further, as might be expected given the importance of vegetation structure to birds, climatic effects are partially manifested through plants.

There is a geographical gradient in the MRD of the bird fauna from drier to wetter areas (Fig. 1b,c), with broad spatial covariation between the species richness of a cell and the mean level of evolutionary development of the birds in that cell (cf. Fig. 1a–c). The spatial pattern in MRD is also very similar using both the Sibley & Ahlquist tree and the hybrid tree. This reflects that MRDs in cells are very strongly positively
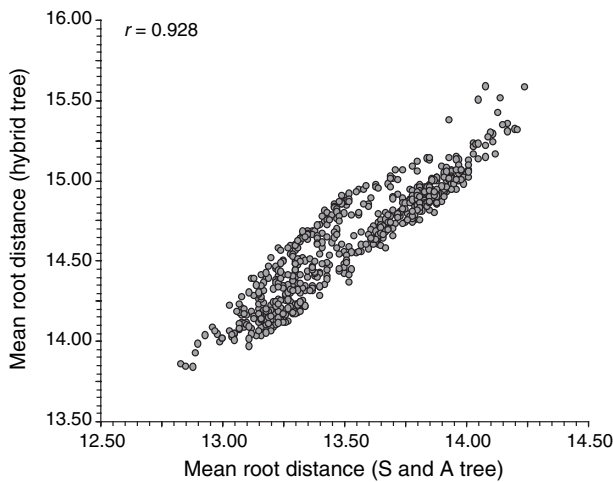
Figure 3 Relationship between mean root distances in 110 × 110 km cells calculated from Sibley & Ahlquist's (1990) tree and from a hybrid tree comprised of the non-passerine tree of Sibley & Ahlquist and the passerine tree of Barker *et al.* (2004).

Figure 4 (a) Relationship between the species richness of birds in 110 × 110 km cells and their mean root distance, based on the tree of Sibley & Ahlquist (1990). Patterns at other grain sizes were statistically indistinguishable, and the observed correlation is higher than 99.9% of the randomized correlations obtained after taking into account that richness is the denominator of MRD. (b) Relationship between species richness and the normalized difference (*Z*-scores), comparing observed and expected MRDs across cells. Black dots denote cells with *Z*-scores that are significantly different (*P* < 0.05) than expected from a random sample of species.

correlated (Fig. 3), so we used the data from Sibley & Ahlquist for further analysis to reduce redundancy.

The visual relationship between richness and MRD is strongly supported statistically (Fig. 4a) and cannot be considered a statistical artefact or due to an intrinsic mathematical relationship between the variables. First, the correlation between richness and *Z*-scores from the randomization tests is also significant and quite similar (Fig. 4b), and second, the observed correlation between richness and MRD is stronger than 99.9% of the correlations obtained by the randomization taking into account the intrinsic dependence between these two variables. Thus, on average, the birds in dry areas (where richness is low) mostly represent more highly derived taxa, with significantly higher MRD than expected by chance alone, whereas the birds in wet areas (where richness is high) also include older, less derived clades, with root distances close to the expected values. It is noteworthy that this pattern exists even in the face of potential dispersal by modern species.

There are various ways that this evolutionary signal in the richness gradient could develop. For example, speciation rates could vary among basal vs. derived groups under different environmental conditions, such that more derived taxa have speciated to a greater extent relative to basal taxa in dry areas than wet areas whereas older taxa have similar speciation rates everywhere. Or, speciation rates may be similar everywhere for all groups, but basal taxa have been differentially extirpated from deserts. Other combinations of differential speciation/extinction rates can also be envisaged, and it is impossible to distinguish the range of alternatives unambiguously without direct measures of speciation and extinction rates. However, although we cannot estimate extinction and speciation rates, we examined variation in the net diversification rates of basal and derived groups by
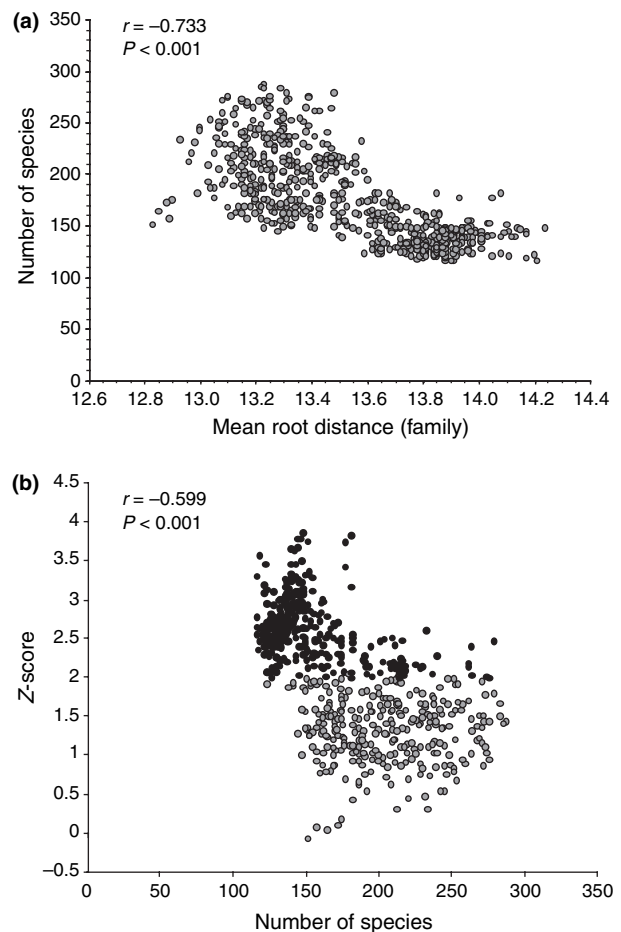
comparing the richness patterns of the most basal quarter of the avifauna against the pattern of the most derived quarter of species. Species-rich areas support more species of both groups (Fig. 5), suggesting that speciation rates are high for all birds in climates currently conducive to high bird richness. Areas of low diversity, in contrast, support fewer species of both basal and derived groups, suggesting that deserts have depressed speciation rates of most bird clades. Further, the ratio of derived to basal groups is higher in low-diversity deserts (*c.* 2 : 1) than in high-diversity wet forests (*c.* 1.1 : 1), suggesting that basal taxa have been prone to extirpation from dry areas. Thus, the pattern of evolutionary development is consistent with the interpretation that areas currently supporting forest have served as centres of diversification of
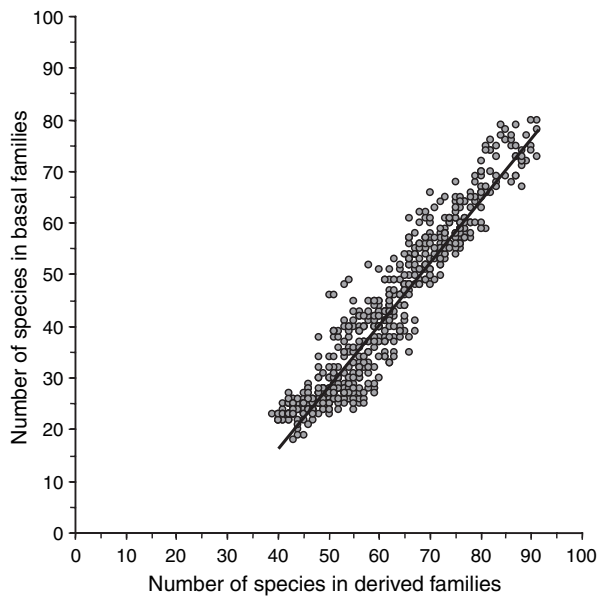
Figure 5 Relationship between the number of species from derived families vs. the number from basal families in 110×110 km cells. The 527 bird species were ranked from the most basal to the most derived clades (resolved to family), and the approximate 25% and 75% percentiles were selected (141 species from basal families and 132 species from derived families). There is a strong correspondence between the numbers of each group, such that cells of high richness contain large numbers of species of both groups, whereas both groups are less well represented in areas of low richness. The slope of the relationship was obtained using a restricted major-axis model II regression and is significantly greater than beta = 1.0 (1.245 ± 0.015; $v^* = 6.6$; $P < 0.001$), suggesting that species from basal families are lost from areas of low diversity at a faster rate than species from more derived families.

all birds, both primitive and derived, whereas areas currently comprising desert suffer from depressed speciation rates, perhaps coupled with increased extinction rates in which primitive groups have been especially affected. But if so, why should older, more primitive birds be more extinction prone in dry habitats?

It is generally agreed that the entire continent was warm and wet during the Cretaceous and early Tertiary (Kemp, 1978; Christophel & Greenwood, 1989; White, 1994) and was mostly covered by forest (Christophel & Greenwood, 1989; White, 1994). However, by perhaps 25,000,000 yr BP, the continent began to experience increasing aridity in the north and north-west, with major decreases in precipitation at the end of the Miocene and into the Pliocene. This climate change is well known to have been associated with major extinction events within the continent; for example, approximately one-third of mammal families present in the Miocene were lost in the end of the epoch (Tedford, 1985). Thus, it is clear that the long-term shift in rainfall patterns occurring during the Miocene and Pliocene had a profound impact on speciation and extinction rates in Australia, but the extent

that these events have left an imprint on the contemporary richness pattern within the continent has not been quantified, as far as we know. The fact that a spatial pattern in the mean evolutionary development of local and subregional avifaunas can be observed even millions of years after the decrease in forest cover since the Miocene suggests that evolutionary patterns persist even in taxa where dispersal might be expected to mask such effects quickly. Further, finding that the newer arid and semi-arid habitats support relatively more derived taxa whereas the relictual forests support relatively more basal taxa indicates that it is likely that the selective loss of bird species from older groups in drier areas reflects an inability of many clades (families) that initially evolved under wetter conditions to adapt to continental-scale climate change, having survived largely in areas where high rainfall and abundant vegetation persisted. A very similar argument has been developed for floral patterns in western Australia (Hopper *et al.*, 1996), but that it is also apparent in birds indicates that it is possible to extract the historical signal underlying richness gradients of even highly mobile groups.

Although it is clear that climate change must be at least partially responsible for the evolutionary patterns, the possibility that other factors have also influenced the diversity gradient is apparent in western Australia. Although richness and MRD are negatively correlated across the continent, there is a set of five anomalous points (at the lower left in Fig. 4a). These represent the cells in the extreme south-west, where richness is moderately low but dominated by more basal families (Fig. 1). Thus, it appears that as the deserts spread in central Australia, this small, productive area became isolated from the major centre of bird diversification in the east, implicating geographical isolation, area, or both, as being locally important. Again, this is similar to patterns for plants (Hopper *et al.*, 1996).

A spatial correspondence of evolutionary and ecological components of species richness suggests that arguments that only current conditions or only historical conditions influence diversity gradients are probably incorrect. Further, the contemporary pattern of diversity in Australia is strongly associated with current levels of water availability, whereas the phylogenetic pattern is associated with reduction in water levels over millions of years, thereby identifying water as a primary driving variable for both past and contemporary diversity patterns in a warm part of the world (Hawkins *et al.*, 2003b). Thirdly, the observed link between water, species richness and MRD could be interpreted as evidence that evolutionary time is an important component of climate–energy relationships; areas that have been warm and wet for long periods of time support more species than areas that become cold or dry (Hawkins, 2004). Finally, it appears that the answer to the question of whether regions of high biodiversity represent cradles or museums (Jablonski, 1991; Chown & Gaston, 2000) is that they are both, at least in the case of Australian birds. Although climate influences extinction rates, we reiterate it is not yet fully understood

which of several possible mechanisms can result in higher speciation rates in warm and wet climates. Despite this, evidence is accumulating that water–energy balance represents a key component of the explanation for the non-random distribution of species on the planet both past and present.

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BIOSKETCHES

Bradford A. Hawkins is interested in biogeography and macroecology, with a major emphasis on broad-scale diversity gradients.

José Alexandre F. Diniz-Filho is interested in statistical methods applied to macroecology and evolutionary biology. He is also interested in the application of spatial statistics to define operational units for intraspecific conservation and to establish priority areas for conservation.

Stephen A. Soeller is a research computing specialist and has developed and managed Geographic Information System products and programs over the past 14 years.

Editor: Philip Stott