Global patterns in endemism explained by past climatic change

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I propose that global patterns in numbers of range-restricted endemic species are caused by variation in the amplitude of climatic change occurring on time-scales of 10–100 thousand years (Milankovitch oscillations). The smaller the climatic shifts, the more probable it is that palaeoendemism survive and that diverging gene pools persist without going extinct or merging, favouring the evolution of neoendemism. Using the change in mean annual temperature since the last glacial maximum, estimated from global circulation models, I show that the higher the temperature change in an area, the fewer endemic species of mammals, birds, reptiles, amphibians and vascular plants it harbours. This relationship was robust to variation in area (for areas greater than 10^4 km²), latitudinal position, extent of former glaciation and whether or not areas are oceanic islands. Past climatic change was a better predictor of endemism than annual temperature range in all phyla except amphibians, suggesting that Rapoport's rule (i.e. species range sizes increase with latitude) is best explained by the increase in the amplitude of climatic oscillations towards the poles. Globally, endemic-rich areas are predicted to warm less in response to greenhouse-gas emissions, but the predicted warming would cause many habitats to disappear regionally, leading to species extinctions.

Keywords: biodiversity; extinction; geographical range size; macroecology

1. INTRODUCTION

Given that endemism (the number of species endemic or confined to an area) and extinction risk are closely coupled (IUCN 2001), actions to minimize global extinction need to focus on patterns in endemism and range-restricted species (Myers *et al.* 2000; Pimm & Brooks 2000; Pimm *et al.* 1995). Most species are not scientifically described (May 2000), and consequently nothing is known about their ecology or geographical distributions (Pimm & Brooks 2000). However, present knowledge of species and their geographical distributions must be used to elucidate the causes of patterns in endemism. The number of taxa endemic to an area increases with its size and isolation (Anderson 1994). Hotspots of range-restricted endemic species have also been proposed to concur with peaks in long-term climatic stability (Fjelds 1995; Cronk 1997; Fjelds & Lovett 1997a). However, long-term stability has been inferred only indirectly from the presence of relict species (Fjelds 1995; Fjelds & Lovett 1997b) or from current between-year climatic stability (Fjelds *et al.* 1997, 1999). Climatic variability among years has pronounced peaks on the time-scale of 10–100 thousand years (kyr) owing to periodical changes in the Earth's orbit, termed Milankovitch oscillations (Imbrie *et al.* 1989; Webb & Bartlein 1992). Such climatic shifts lead to large changes in species' geographical distributions termed orbitally forced range dynamics (ORD) (Dynesius & Jansson 2000; Jansson & Dynesius 2002). The magnitude of ORD varies depending on the level of climatic shifts and whether or not local environmental conditions buffer against regional climatic change. I propose that the lower the level of ORD

in an area, the more range-restricted species it may harbour (Dynesius & Jansson 2000; Jansson & Dynesius 2002), resulting in higher endemism than similar-sized climatically more variable areas. Low levels of ORD enable survival of ancient lineages that have become extinct in other areas (palaeoendemism) (Fjelds *et al.* 1999), as well as preservation of the genetic variation within those persisting populations (Templeton 1998). Moreover, neoendemic species are more likely to evolve (Dynesius & Jansson 2000; Jansson & Dynesius 2002): the smaller the climatic shifts in an area, the more probable it is that new clades persist, without going extinct or reuniting with other clades (Cronin 1985; Futuyma 1987; Glazier 1987; Dynesius & Jansson 2000), irrespective of what caused the cladogenesis. Moreover, if ORD is low, species with low vagility (low dispersal ability and propensity) and high specialization may evolve, and such species are more likely to have small range sizes (Dynesius & Jansson 2000). To test the theory that orbitally forced climatic variability reduces endemism, I used data on the number of endemic species in geopolitical units of the world, and estimates of long-term temperature change from general circulation models (GCMs). Geographically, levels of endemism are higher in the tropics (Gentry 1986; Stattersfield *et al.* 1997) and on oceanic islands, but, to my knowledge, global patterns in the relationships between endemism and environmental factors have not been examined before.

The main competing (or complementary) theory to explain global patterns in the distribution of range-restricted species is that species' geographical range sizes increase with an increasing range of seasonal changes. Seasonal environmental variation sets the minimum breadth of tolerances required by individuals at a given site, enabling species with individuals adapted to high seasonality to attain larger range sizes (Stevens 1989). Larger range sizes result in lower endemism since fewer species

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are confined to a specific area. Thus, a negative relationship between endemism and degree of seasonal change is expected. I tested the relative effects of past climatic change, climatic seasonality and the degree of isolation (whether or not an area is an oceanic island) on endemism.

Here, I show that the higher the estimated temperature change in an area since the last glacial maximum (LGM) *ca.* 21 kyr ago, the fewer endemic species it harbours. This relationship was robust to variation in area once it exceeded 10^4 km², and remained after taking extent of former glaciation and latitudinal position into account. Temperature change was a better predictor of endemism than was annual temperature range or whether or not an area was an oceanic island. Endemic-rich areas are predicted to be less affected by global warming over the next 100 years than endemic-poor ones, although the predicted warming would lead to large habitat alterations, threatening many narrowly distributed species with extinction.

2. DATA AND METHODS

(a) *Measuring geographical patterns in Milankovitch climate oscillations*

Data on the magnitude of long-term climatic change lack the geographical coverage to allow comparison among many areas. Instead, I used temperature change between the present and the LGM estimated from GCMs as a measure of the magnitude of Milankovitch climatic change. This interval represents almost the entire temperature range attained during the Quaternary (Imbrie *et al.* 1989), and forced large changes in species' geographical distributions (Bennett 1997; Webb & Bartlein 1992). In GCMs, modern climates are modelled from observational data. When modern climates can be accurately predicted, parameters are set and the model run with LGM values. I used change in mean annual surface-air temperature estimated by three different GCMs, denoted 'GISS' (Hansen *et al.* 1983; data obtained from Rind (1994)), 'CCM1' (Kutzbach *et al.* 1998; data obtained from Kutzbach *et al.* (1996)) and 'UVic' (Weaver *et al.* 1998). The GCMs differ in input parameters and modelling procedure. Using data from several GCMs reduces the risk that the results are compromised by errors and idiosyncrasies of individual GCMs. The spatial resolution is $7.8^\circ \times 10.0^\circ$ (latitude versus longitude) for GISS, $4^\circ \times 7.5^\circ$ for CCM1 and $3.75^\circ \times 1.855^\circ$ for UVic. Thus, they predict regional rather than local climates. I focused on temperature change, ignoring changes in precipitation, which are undoubtedly important, but show more complex temporal patterns (Kutzbach *et al.* 1998). Although precipitation has changed considerably since the LGM, there is no evidence for pronounced large-scale *spatial gradients* in the degree of precipitation change between the present and the LGM in the output of the models used.

I tested whether temperature change since the LGM, estimated from GCMs, can be taken as a measure of the amplitude of temperature change on Milankovitch time-scales, using estimates of sea-surface temperatures covering *ca.* 300 kyr (Imbrie *et al.* 1989). In these records, using composition of foraminiferans from sediments as a proxy, the difference in temperature between the most recent record and LGM ones is significantly positively correlated with the amplitudes of temperature variability caused by Milankovitch oscillations having 100 kyr and 41 kyr time-periods (figure 1). Changes in these two frequency bands have dominated Quaternary climatic variation (Webb &

Figure 1. The change in sea-surface temperatures between the present and the LGM *ca.* 21 kyr ago increases with temperature variance in (a) the 100 kyr frequency band ($r = 0.74$, $p < 0.001$), and (b) the 41 kyr frequency band ($r = 0.66$, $p < 0.01$). Sea-surface temperatures were estimated from compositional variation of foraminiferans during the last *ca.* 300 kyr obtained from 17 sediment boreholes in the Atlantic and Indian Oceans (Imbrie *et al.* 1989). The species composition of foraminiferans varies with temperature, allowing inferences about temperature change. Each point represents a sediment borehole site. Coherent amplitude is the variance that is linearly correlated with variation in the Earth's orbit with a specific time period, here 100 and 41 kyr (Imbrie *et al.* 1989).

Bartlein 1992). Moreover, the changes in mean annual surface-air temperatures since the LGM, estimated by the three GCMs described above, were significantly positively correlated with the change in foraminiferan-estimated sea-surface temperatures since the LGM (GISS: $r = 0.73$; CCM1: $r = 0.55$; UVic: $r = 0.62$; 17 sites, $p < 0.05$), as well as with the amplitude of change in sea-surface temperatures in the 100 kyr and 41 kyr frequency bands (GISS: $r_{100 \text{ kyr}} = 0.75$ and $r_{41 \text{ kyr}} = 0.85$;

CCM1: $r_{100 \text{ kyr}} = 0.73$ and $r_{41 \text{ kyr}} = 0.77$; UVic: $r_{100 \text{ kyr}} = 0.58$ and $r_{41 \text{ kyr}} = 0.72$; 17 sites, $p < 0.01$). Thus, geographical patterns in temperature change between the present and the LGM from GCMs are representative of geographical patterns in the amplitude of temperature variation over longer time-scales, and can be used as proxies for climatic variability on Milankovitch time-scales.

(b) Data on endemism and species richness

To test the theory that endemism is negatively associated with the amplitude of Milankovitch climate oscillations, I used data on the number of endemic species and the total species numbers of mammals, birds, reptiles, amphibians (World Conservation Monitoring Centre 1994) and vascular plants (Davis *et al.* 1994–1997) in different geopolitical units of the world, mostly countries. The data on endemism in the sources used reflect the state of knowledge at the time of their completion. Subsequently, in some cases, numbers of endemics per geopolitical unit have changed owing to taxonomic revision and increased knowledge about species' geographical distributions. The areas range in size from Monaco (2 km²) to the former Soviet Union (22 400 000 km²), with a median size of 78 864 km². The number of endemic species depends on area in two ways. First, total species number increases with area, and more endemics are expected the more species there are. Second, the proportion of species endemic to an area increases with its size, as increasingly more species are confined to it. Counts of species numbers and area sizes were log-transformed before analysis to better fit a normal distribution.

Since larger areas harbour more endemics, I factored out the effect of area in the analyses by partial correlation or regression (in log-log space, by calculating the correlation between each variable and area, or by regressing each variable on area, and then using the residuals in the further tests). The residuals thus obtained represent the relative density of endemics. I classified all geopolitical units into oceanic islands (i.e. if they had no land-bridge during the sea-level low of the last ice age) or parts of mainlands, according to Peltier (1994). Australia was classified as an island. Oceanic islands were, on average, three orders of magnitude smaller than mainland areas (median island size 749 km², 92 islands; median mainland-area size 207 600 km², 171 areas; $p < 0.0001$, Mann–Whitney *U*-test).

(c) Testing for patterns in endemism and species richness

I tested for partial correlations (controlling for variation in area) between the number, and the proportion, of endemic species and the midpoint of change in GCM-estimated mean annual surface-air temperature between the present and the LGM for each geopolitical unit. Temperature data were log-transformed before analysis. I also tested for correlations between the numbers of endemic species per area in different phylads (i.e. mammals to plants), and for correlations between the number and the proportion of endemics per area. Moreover, I tested for correlations between the number, and the proportion, of endemics and the total species richness per area. Finally, I tested for correlations between total species richness of each phylad and temperature change.

To test the robustness of the area correction, I divided the areas into four size classes, i.e. areas less than 10⁴ km², 10⁴–10⁵ km², 10⁵–10⁶ km² and greater than 10⁶ km². Oceanic islands dominated the smallest size classes (69 out of 82 areas), but were few in the larger ones (11 out of 58, 10 out of 90 and 2

out of 33, respectively). I also tested for a correlation between area and latitudinal position.

I used path analysis (Wright 1921; Shipley 2000) to test the relative importance of temperature change since the LGM, annual temperature range (FAO 1997) and whether or not an area is an oceanic island ('islandness') on the degree of endemism per area. If the annual temperature range varied within a geopolitical unit, I took the midpoint value. In path analysis, explicit assumptions are made about the causal relationships among variables by specifying causal linkages between them. Mathematically, it is equivalent to a series of linear regressions. The technique allows decomposition of the overall correlation between two variables into direct effects of one on the other, indirect effects mediated by other variables and non-causal components resulting from common causes. Path analysis assumes that all important variables are identified, that effects are linear, additive and unidirectional, and that residuals are uncorrelated (Sokal & Rohlf 1995). I propose that the level of past temperature change, annual temperature range and islandness affect the degree of endemism per area either directly, or indirectly by varying with latitude.

(d) Future global warming

To assess the relationship between global patterns in endemism and future human-induced climatic change, I tested for partial correlations (controlling for variation in area) between endemism and the warming predicted to occur over the next 100 years per geopolitical unit. I used warming in mean annual surface-air temperatures predicted to occur between the periods 1961–1990 and 2070–2099 from the UK Hadley Centre GCM, assuming that greenhouse-gas emissions are not reduced (HadCM3 GGA1, data archived at <http://www.cru.uea.ac.uk/link/index.htm>). For each geopolitical unit, I took the midpoint value. Values were log-transformed prior to analysis to better fit a normal distribution.

3. RESULTS AND DISCUSSION

(a) Relationship between endemism and species richness

The level of endemism per area was correlated across phylads, ranging from $r = 0.64$ to $r = 0.82$ in pairwise comparisons between phylads (i.e. mammals to plants, ≥ 167 areas, the exact number of areas varied depending on data availability, holding area constant, $p < 0.0001$), suggesting that endemism is governed by similar processes in all phylads. The number of endemics per area increased with total species richness in all phylads ($r = 0.39$ to $r = 0.91$ for ≥ 45 islands, and $r = 0.43$ to $r = 0.77$ for ≥ 101 mainland areas, holding area constant, $p < 0.01$). Moreover, the number and the proportion of endemics (arcsin-square-root transformed values) were positively correlated in all phylads ($r = 0.74$ to $r = 0.87$, holding area constant, $p < 0.0001$). The result that numbers of endemic species and total species numbers are correlated may result from the relatively low resolution of the data, since studies with higher spatial resolution demonstrate only weak correlations between numbers of narrowly distributed species and total species richness (Jetz & Rahbek 2002).

(b) Endemism and total species richness versus temperature change since the LGM

The number of endemics per area of all phylads decreased with increasing GCM-estimated temperature

change since the LGM (figure 2), thus supporting the theory that Milankovitch climate oscillations and high levels of ORD reduce endemism. All three GCMs produced similar results, and temperature estimates from GISS only are reported. Moreover, using the proportion instead of the number of endemics did not change the results in these and all subsequent analyses, and results for only the numbers of endemics are reported. The negative correlations did not arise simply because areas that were covered by glaciers or polar deserts during the last glacial period have few endemics (figure 2). Although such areas

Figure 2. Endemism per unit area in mammals, birds, reptiles, amphibians and vascular plants decreases with increasing temperature change since the LGM. Each circle represents a geopolitical unit. Open circles: areas covered by glaciers or polar deserts during the last glacial period; filled circles: remaining areas. The relationship between the number of endemic species and the change in mean annual surface-air temperatures since the LGM for: (a) mammals ($r = -0.46$, 223 areas); (b) birds ($r = -0.46$, 226 areas); (c) reptiles ($r = -0.57$, 224 areas); (d) amphibians ($r = -0.47$, 225 areas); and (e) vascular plants ($r = -0.46$, 198 areas). All correlations are partial correlations, holding area constant, and significant at $p < 0.0001$. Values are non-standardized residuals from regressions (using log-transformed values) to factor out the effect of area.

have few endemics, the negative correlations between endemism and temperature change remained in all phylads after excluding once glaciated or polar-desert areas, classified after Adams (1997) ($r = -0.39$ to $r = -0.54$, holding area constant, ≥ 185 areas, $p < 0.0001$). The total number of species decreased with increasing temperature change since the LGM for mainland areas ($r = -0.36$ to $r = -0.84$, holding area constant, ≥ 102 areas, $p < 0.0001$), but the relationship was non-significant ($p > 0.05$) for islands in all phylads except reptiles ($r = -0.37$, $p = 0.005$, 54 islands).

(c) Sensitivity tests

Although the effect of area was factored out of the analyses, the large variation in area might have confounded the results. Therefore, I performed sensitivity tests of the area correction. The size of geopolitical units on mainlands did not vary significantly with latitude ($r = -0.04$, 171 areas, $p = 0.65$), but the size of oceanic islands increased somewhat with latitude ($r = 0.24$, 92 islands, $p = 0.02$). Small islands were biased towards low latitudes, many being coral atolls, which are absent outside the tropics.

The negative relationship between endemism and temperature change was robust to variation in area, and remained across more than two orders of magnitude of variation in area. For areas less than 10^4 km² in size (82 areas, 69 of which are islands), endemism-temperature-change relationships were weak, being significant for only birds ($r = -0.45$, $p < 0.0001$) and reptiles ($r = -0.26$, $p < 0.05$), and nearly significant for plants ($r = -0.23$, $p = 0.06$). These areas had few or no endemics in all phylads, and thus the variance in numbers of endemics between areas was low, irrespective of whether areas were islands or not. For the 58 areas (11 of which are islands) 10^4 – 10^5 km² in size, the number of endemics decreased strongly with increasing temperature change ($r = -0.47$ to $r = -0.69$, holding area constant, ≥ 37 areas, $p < 0.0001$). This was also true for the 90 areas (10 of which are islands) 10^5 – 10^6 km² in size ($r = -0.34$ to $r = -0.58$, ≥ 63 areas, $p < 0.0001$), as well as for the 33 areas (two islands) greater than 10^6 km² in size ($r = -0.63$ to $r = -0.85$, ≥ 24 areas, $p < 0.001$). The number of endemics on islands greater than 10^4 km² decreased with increasing temperature change in all phylads ($r = -0.48$ to $r = -0.68$, ≥ 15 areas, $p < 0.05$). Thus for areas greater than 10^4 km² in size, the pattern was robust, irrespective of whether areas

Figure 3. Path diagram for (a) mammals; (b) birds; (c) reptiles; (d) amphibians and (e) vascular plants, for the effects of past climatic change (temperature change since the LGM), annual temperature range and whether or not an area is an oceanic island on endemism per unit area. The correlations between the predictor variables and endemism were assumed direct or indirect by varying with latitude. The residual variables (U_1 and U_2) represent the unmeasured factors affecting endemism and latitude. The relationships are assumed to be unidirectional causal (single-headed arrows), or left as non-analysed correlations (double-headed arrows). Path coefficients are standardized partial regression coefficients from linear regressions.

rowly distributed species did not count as endemics. Second, endemism is incompletely known and probably underestimated in many climatically relatively stable tropical countries (Gentry 1986). These two factors are likely to lead to underestimation of the strength of the relationship rather than to cause it. Third, there might be errors in the temperature changes estimated by the GCMs, as discussed in § 3f.

(d) The relative importance of different factors for endemism

The three predictor variables in the path analyses together accounted for 66–77% of the variation in latitude ($R^2_{\text{adj}} = 0.66$ to $R^2_{\text{adj}} = 0.77$; values varied among phylads depending on for which geopolitical units endemism data were available) (figure 3), suggesting that these variables can explain decreases in endemism with increasing latitude without invoking other, unknown variables covarying with latitude. In table 1, the correlations between endemism and the predictor variables are decomposed into direct effects and indirect effects via latitude. Past climatic change had the highest effect coefficient for mammals, birds, reptiles and plants, being negatively correlated with endemism (table 1). The indirect path via latitude accounted for 24–41% of the strength of the effect coefficient for mammals, birds and reptiles, whereas this path accounted for only 2% in plants (table 1). The effect coefficients for annual temperature range were small in the path analyses of all phylads except amphibians, because positive direct components were cancelled out by negative indirect ones via latitude (table 1). For amphibian endemism, the effect coefficient of annual temperature range was stronger than that of past climatic change, both being negatively correlated with endemism (table 1). The variance inflation factors of the predictor variables of endemism were larger than the model variance inflation factors in the path analyses of all phylads (largest factor = 4.51), suggesting effects of collinearity (Petraitis *et al.* 1996). However, when each of the predictor variables was successively left out, the remaining path coefficients remained similar, suggesting that collinearity did not confound the results. The assumption in the path analyses that past climatic change, annual temperature range and islandness would have direct causal effects on latitude (figure 3) should not be taken literally. These variables cannot affect latitudinal position any more than latitude by itself can have a causal effect on endemism. Instead, 'latitude' should be interpreted as the components of the predictor variables covarying with latitude (together with other fac-

were islands or not. The absence of pattern in the smallest size class, primarily consisting of islands, is probably because their small populations have high extinction rates irrespective of the amplitude of climatic shifts, preventing endemics from accumulating.

Three factors reduced the precision of the analyses. First, geopolitical boundaries are essentially arbitrary in relation to species range limits, meaning that many nar-

Table 1. Correlations with endemism per unit area decomposed into direct and indirect effects, and the sum of these coefficients, i.e. the effect coefficients.
(The direct and indirect effects are calculated by summing the path coefficients following the arrows in figure 3. Indirect effects are paths via latitude.)

variables in correlation		direct effect	indirect effect	effect coefficient
mammal endemism	past climatic change	−0.23	−0.16	−0.39
	annual temperature range	0.18	−0.20	−0.03
	island (yes or no)	0.14	−0.13	0.01
	latitude	−0.32	0.00	−0.32
bird endemism	past climatic change	−0.22	−0.07	−0.29
	annual temperature range	0.05	−0.10	−0.04
	island (yes or no)	0.25	−0.06	0.19
	latitude	−0.15	0.00	−0.15
reptile endemism	past climatic change	−0.25	−0.15	−0.40
	annual temperature range	0.06	−0.21	−0.14
	island (yes or no)	0.11	−0.13	−0.02
	latitude	−0.31	0.00	−0.31
amphibian endemism	past climatic change	−0.14	−0.12	−0.26
	annual temperature range	−0.14	−0.16	−0.30
	island (yes or no)	−0.04	−0.10	−0.14
	latitude	−0.25	0.00	−0.25
plant endemism	past climatic change	−0.50	0.01	−0.49
	annual temperature range	0.08	0.01	0.09
	island (yes or no)	−0.01	0.01	−0.01
	latitude	0.02	0.00	0.02

tors, denoted by U_2 in figure 3) that have an effect on endemism.

The fact that endemism of mammals, birds, reptiles and plants is more strongly correlated with past climatic change than with annual temperature range suggests that the increase in species' range sizes towards higher latitudes, called Rapoport's rule (Stevens 1989), is better explained by Milankovitch climate oscillations forcing larger distributional changes (Dynesius & Jansson 2000), than by higher tolerances to current environmental variation. Rapoport's rule is most prominent north of approximately 40° N (Gaston 1999), where the latitudinal gradient in temperature change since the LGM is steepest (Imbrie *et al.* 1989; Kutzbach *et al.* 1993, 1996; Rind 1994; Weaver *et al.* 1998). Moreover, because there is little latitudinal variation in mean annual temperature in the tropics (from approximately 25° N to 25° S), species can attain large ranges despite low temperature tolerance (Terborgh 1973), which would counteract the putative effect of annual temperature range on species' range sizes.

According to the path analyses, islandness had a small effect on endemism in all phylads except birds and amphibians (table 1). Temperature change since the LGM was lower on oceanic islands than mainlands (92 islands (mean ± s.e.): 1.8 ± 0.25 °C; 171 mainlands: 5.4 ± 0.39 °C; $p < 0.0001$, Mann–Whitney U -test). This partly explains the low coefficients of islandness in the path analyses (table 1). Although the primary reason for high endemism on islands is doubtless their isolation, oceanic climates buffering against long-term climatic extremes may also play a part (Cronk 1997) in allowing incipient neoendemic and old palaeoendemic species to survive.

- (e) *Future global warming*
- Endemic-rich areas are predicted to warm less in response to greenhouse-gas emissions over the next 100 years than endemic-poor ones. I found significant negative correlations between the number of endemics and the level of future warming for all phylads (mammals: $r = -0.37$, $n = 217$; birds: $r = -0.49$, $n = 221$; reptiles: $r = -0.38$, $n = 220$; amphibians: $r = -0.26$, $n = 221$; plants: $r = -0.24$, $n = 168$; $p < 0.001$ in all cases, partial correlations of log-transformed values, holding area constant). This is perhaps not surprising as endemic-rich areas are those that have previously been least affected by global climatic change. However, even the most stable areas are predicted to warm 3–5 °C according to the model used, which would exceed the tolerance of many species. Most species have survived previous climatic shifts by, primarily, tracking their preferred habitat through space, or by inhabiting climatically stable areas (Bennett 1997). However, the rapid human transformation of the Earth's ecosystems will make habitat tracking in response to climatic change more difficult (Coope 1995). Most living species have experienced global temperatures as warm as today's for less than 5% of the last three million years (Webb & Bartlein 1992). The habitats of many species, for example, cloud forests on mountain tops, may disappear regionally, leading to species extinctions (Pounds *et al.* 1999).
- (f) *Evaluating the robustness of the endemism–temperature-change relationship*
- According to cooperative projects, such as the Paleoclimate Modeling Intercomparison Project (Pinot *et al.* 1999), there is high general correspondence among

GCMs in their predictions of past environments (Webb 1998; Guiot *et al.* 1999; Pinot *et al.* 1999; Valdes 2000; Kageyama *et al.* 2001). The large-scale patterns of temperature change since the LGM predicted by the GCMs are in agreement with estimates from palaeodata, although there are discrepancies in the predictions of absolute values (Webb 1998; Guiot *et al.* 1999; Pinot *et al.* 1999; Valdes 2000; Kageyama *et al.* 2001). However, for the endemism–temperature-change relationship to be valid, absolute values of glacial cooling need not be correctly predicted, provided the global spatial pattern of cooling is reproduced correctly. For example, the level of tropical cooling at the LGM is lower in GCMs utilizing prescribed LGM sea-surface temperatures estimated from foraminiferal data (such as GISS), than is indicated by other palaeodata (Guiot *et al.* 1999; Pinot *et al.* 1999). Nevertheless, such GCMs share basic features of the spatial patterns of LGM cooling with GCMs in which sea-surface temperatures are estimated by the model (e.g. CCM1 and UVic), predicting higher levels of tropical cooling. These common features include more cooling towards higher latitudes, close to ice sheets, and over land compared with oceans in the tropics (Rind 1994; Kutzbach *et al.* 1996; Weaver *et al.* 1998).

How would incorporation of changes in precipitation since the LGM affect the relationship between endemism and past climatic change? GCMs and palaeodata indicate that the LGM was drier than present climates in most regions and that variation in the intensity of monsoons since the LGM has caused additional variation (Kutzbach *et al.* 1998). Despite large temporal changes in precipitation, there is no indication in the GCMs of large-scale spatial patterns in precipitation change since the LGM that could override patterns in temperature (Hansen *et al.* 1983; Rind 1994; Kutzbach *et al.* 1996, 1998; Weaver *et al.* 1998).

(g) Support from regional-level studies and evolutionary implications

I found highly significant correlations between endemism and levels of past climatic change, despite the imprecision of the data on both factors. Although global patterns of endemism have not been related to the magnitude of past climatic change before, a number of regional-scale studies support the findings. In tropical South American and African birds, and in Afrotropical plants, the richness of both palaeoendemic and neoendemic species peaks in areas, for example, montane forests, where climatic stability is high (Fjelds 1994, 1995; Fjelds & Lovett 1997b) because local factors buffer against regional climatic change (Fjelds 1995; Fjelds *et al.* 1997, 1999). The local moderation of climatic extremes is likely to have persisted through the shifting climates of the Quaternary, permitting gene pools to survive and maintain their integrity. In the floras of sub-Saharan Africa and Australia, the centres of range-restricted plant species are located in areas that were buffered against climatic extremes (Crisp *et al.* 2001; Linder 2001). In New Zealand alpine plants, endemism peaks in areas that provided habitat continuity through Quaternary climatic oscillations (McGlone *et al.* 2001).

This study supports the notion that ORD is an important factor in evolution (Jansson & Dynesius 2002).

A large proportion of all species have small geographical distributions. For example, 27% of all bird species in the world have range sizes smaller than 50 000 km² (Stattersfield *et al.* 1997). The importance of ORD might not be limited to patterns in species' range sizes, but ORD may be a major factor shaping the size and characters of regional assemblages of taxa (Dynesius & Jansson 2000; Jansson & Dynesius 2002).

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