LETTER

Global variation in diversification rates of flowering plants: energy vs. climate change

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Abstract
We used the largest DNA-based phylogeny of flowering plants to date to evaluate the importance of energy vs. past climate change in predicting global patterns in diversification. Relative diversification rates increased towards the equator, suggesting that differences in per-lineage net diversification may be an important component of the latitudinal diversity gradient. The amplitude of Quaternary climate oscillations experienced by families explained variation in diversification equally well compared to contemporary energy measures, and energy and climate change measures were intercorrelated, making it difficult to reject either as a causal mechanism. Many putative mechanisms linking diversification to energy availability do not apply to plants, whereas the climate change mechanism has more support. We also present the first global map of angiosperm diversification, showing that, after correcting for family range-size, tropical diversification rates were fastest for clades currently in regions with high endemic species richness outside the main lowland rainforest areas.

Keywords
Climatic stability, diversification, energy availability, extinction rate, latitudinal gradient, orbitally forced range dynamics, productivity, speciation rate, temperature.


INTRODUCTION

The latitudinal gradient in species diversity, with decreasing number of species going from the equator towards the poles, is one of the most ubiquitous biodiversity patterns, and is documented for most major clades (Hillebrand 2004). Despite a considerable body of research about which factors cause this gradient, it remains a puzzle, lacking a generally accepted explanation. Although the generality of the pattern may suggest a common cause, a multitude of factors vary with latitude making sorting among potential causes difficult. In explaining large-scale diversity patterns, a distinction is often made between contemporary processes setting limits on coexistence, usually some measure of energy availability, and what have been termed historical processes, i.e. the imprint of past events and conditions (e.g. Ricklefs 1987; Jansson 2003; Wiens & Donoghue 2004). This has been useful in emphasizing the likely multiple and complex causes for diversity patterns (e.g. Jetz et al. 2004; Svenning & Skov 2005). However, we argue that it is important to consider both processes simultaneously. Present day patterns of regional species richness will necessarily be a product of the interaction between speciation, extinction, migration and ecology, i.e. historical and contemporary processes.

Differences in diversity may arise as a consequence of variation in times for species accumulation, for example, because of long-term environmental oscillations (Fischer 1960; Wiens & Donoghue 2004), higher diversification rate (speciation minus extinction) in some areas over others (Rohde 1992; Dynesius & Jansson 2000; Davies et al. 2004a–c), or because local conditions vary in their capacity to support multiple coexisting species (Brown 1981). Many studies have documented strong correlations between plant species diversity and measures of energy availability at continental to global scales (e.g. O’Brien 1998; Francis & Currie 2003). However, it is not clear whether such energy-richness relationships are causal, as any variable that co-varies with latitude will tend to correlate closely with species richness, and few studies have directly tested likely mechanisms. Recently, Dynesius and Jansson (Dynesius & Jansson 2000; Jansson & Dynesius 2002) suggested that the latitudinal diversity gradient may be a product of a latitudinal gradient in the amplitude of climatic shifts on time-scales of 10–100 kyr caused by variation in Earth’s orbit and axial tilt, so-called Milankovitch oscillations. Climate change due...
to Milankovitch oscillations has been a feature of Earth’s entire history, although more pronounced during the Quaternary (Webb & Bartlein 1992). The larger the amplitude of climatic shifts during each oscillation, the greater the dynamics in the size and location of species ranges (Webb & Bartlein 1992; Bennett 1997; Dynesius & Jansson 2000). Dynesius and Jansson argued that elevated range dynamics may both increase extinction rates as species fail to disperse or lose their habitat, and reduce speciation rates as diverging gene pools suffer higher risk of extirpation or become blended (Dynesius & Jansson 2000; Jansson & Dynesius 2002).

Here, we evaluate the relative importance of measures of energy availability vs. climate change for diversification in flowering plants. First, we ask whether there is a latitudinal variation in diversification rates consistent with the latitudinal gradient in species richness. Second, we test whether global patterns in diversification rates are better explained by contemporary energy measures or by the inferred degree of orbitally forced range dynamics (Dynesius & Jansson 2000; Jansson & Dynesius 2002), measured as the change in temperature between the present and the Last Glacial Maximum (LGM) c. 21 ka (Jansson 2003). The idea that the latitudinal diversity gradient is caused by increasingly large climatic shifts towards higher latitudes goes back to Wallace (1878), but to the best of our knowledge, no study has tested for a relationship between diversification rates and the degree of climatic oscillations for a major taxon. Finally, to compare diversification rates among regions, we calculated the net rate of diversification per family and present the first map of angiosperm diversification across the globe.

**METHODS**

We used the most comprehensive DNA-based phylogeny of flowering plants to date (Soltis et al. 2000) to explore variation in diversification rates among sister families. First, we calculated the net rate of diversification per family (irrespective of phylogenetic affinity) and used a GIS application to generate a global map of mean angiosperm diversification. Second, following the approach of Davies et al. (2004b), we calculated measures of the contemporary environment and the degree of climate change in the past within the present geographical range of each family. Further, we used regression through the origin (Harvey & Pagel 1991) to test the relative importance of energy availability and past climate change in explaining differences in relative diversification rates between sister families.

**Flowering plant phylogeny**

Using the phylogeny of flowering plants presented by Soltis et al. (2000), we obtained sister-groups representing all pairs of terminal sister families, yielding a total of 86 sister-family comparisons. Sister-group comparisons are one of the best approaches for identifying evolutionary correlates of species richness (Barraclough et al. 1998) since this method avoids problems associated with different ages of clades (sister clades are by definition the same age), non-independence of taxa, confounding variables (e.g. other traits influencing variation in diversification rates; sister clades will differ only in traits evolved since the last common ancestor) and noise (which will most likely mask any relationship between evolutionary variables). Species numbers for families were taken from Davies et al. (2004a).

**Global variation in diversification**

To evaluate geographic patterns in diversification rates among regions, we mapped the number of families and family diversification rates per grid cell on a global map (grain size 1° × 1°) for the 172 families used in the sister-group analysis. The geographic distribution of families was taken from Davies et al. (2004b), originating from Heywood (1993) with corrections. Care should be taken when interpreting fine-scale spatial structure in the variation in diversification rates due to the relatively coarseness of the underlying distribution data. For comparison, we also generated equivalent figures at a grain size of 5° × 5° (see Supplementary Information). Absolute diversification rates were estimated for each family as: ln(species number)/age of family (Magallón & Sanderson 2001). This measure may decrease with increasing age under a homogeneous speciation-extinction process (Ricklefs 2006). Although we found no difference in age between exclusively tropical and non-tropical families ($P = 0.36$, $t$-test), we explored potential for bias by re-estimating diversification rates assuming a constant birth-extinction process:

$$r = 1/t * \log(a[1 - e] + e)$$

following Magallón & Sanderson (2001), where $r$ is the diversification rate and $e$ is the extinction rate. Because we were interested in what effect extinction may have had on our estimates of diversification, we assumed an arbitrarily high value for $e$ of 0.9 [see Magallón & Sanderson (2001) for further justification]. As families with large range-sizes tend to be more species-rich (Gaston & Blackburn 1997; Davies et al. 2004b, 2005), we first regressed diversification rate against range-size, and then plotted the geographical distribution of the residuals. As we have no information on where within the current geographical distribution of a family diversification occurred, our per-cell estimates of diversification rates are likely to be less precise for more wide-ranging families. To address this, and to evaluate whether geographical patterns in diversification rates themselves varied with family range-size, we divided the families...
into quartiles according to range-size (43 families in each quartile), and produced separate maps for each quartile.

**Geographic data**

For each plant family, we recorded latitudinal position, mean annual and seasonal variation in temperature, mean annual evapotranspiration (AET), mean and standard deviation of elevation and the degree of past climate change within the range of the family. Environmental conditions were recorded within the present geographic ranges of each sister clade using GIS software. Ideally, one would use information on paleodistributions and paleoclimates to summarize the environmental conditions experienced by each plant family over their evolutionary history, but such data are lacking. However, documented phylogenetic niche conservatism in climatic tolerance suggests that the geographic ranges of clades will track climatic conditions in space (Wiens & Graham 2005), and hence, the environmental conditions experienced by a family are expected to be consistent through time. Families occupying geographic areas where climatic variation has been large are expected to have experienced larger range shifts as species have tracked changing environmental conditions. This is an explicit assumption of Dynesius and Jansson’s (2002) The dynamics hypothesis (Dynesius & Jansson 2000; Jansson & Dynesius 2002). The assumptions of niche conservatism and environmental tracking are confirmed by paleoecological data (Webb & Barlein 1992; Bennett 1997). Critically, if current distributions did not provide a useful estimate for inferring historical environmental data, it would most likely confound attempts to detect a relationship between diversification and environmental conditions.

Measures of contemporary environment were taken from Davies et al. (2004b). For each measure of the current environment (temperature, AET and elevation), we calculated the mean value for all cells within the geographic distribution of each plant family, as well as the standard deviation of elevation and seasonal variation in temperature. Climate change was measured as the change in mean annual temperature between the present and the LGM estimated from global circulation models (GCMs; data available from the World Data Center for Paleoclimatology, http://www.ncdc.noaa.gov/paleo/model.html). The degree of change over this period is correlated with climatic variability over hundreds of thousands of years for sites across the globe (Jansson 2003). This dynamic climate system is known to have persisted throughout the Quaternary and Pliocene, but a latitudinal gradient in the amplitude of climate shifts should have been present throughout Earth’s history due to the astronomical forcing of climatic shifts. Data from three different GCMs were used to account for variation among models: CCC2 (McFarlane et al. 1992), ECHAM3 (Deutsches Klimarechenzentrum Modellbetreuungsgruppe 1992) and UGAMP (Dong & Valdes 1998). The ability of the GCMs to correctly model past climates is crucial. The Paleoclimatic Modelling Intercomparison Project compared the performance of more than 10 different GCMs against paleoclimatic data (Webb 1998), and found high consistency among models and with paleodata. Although variation in precipitation is likely important for differences in plant species richness, the ability of GCMs to correctly infer precipitation remains poor. In any case, temperature is likely to be correlated with change in general climate, including precipitation, at the global scale.

**Relationship between diversification and environmental variables**

We calculated independent contrasts in species richness and all environmental variables between the sister families. Independent contrasts represent differences between sister clades that have evolved since their last common ancestor (Felsenstein 1985). For each sister pairs A and B, we calculated the species richness contrasts as

\[
\log(a) - \log(b) / \text{age of split}
\]

where \(a\) is species number in A and \(b\) is species number in B. Divergence times were obtained from Davies et al. (2004b) following the protocol outlined by Wikström et al. (2001). Contrasts in environmental variables were calculated as \(X_A - X_B\), where \(X\) is the mean of the environmental variable for a family. Family range-size was cube-root transformed before calculation of contrasts to linearize the relationship between family values of species richness and range-size. We used regression through the origin (Harvey & Pagel 1991) to explore the relationship between contrasts in species richness, the suite of measures of contemporary environment and climate change. To account for phylogenetic uncertainty, we upweighted contrasts for which we had the most confidence (see Davies et al. 2004b). All analyses were performed in the statistical package R (R Development Core Team 2006). To examine the interrelationships among the contrasts in the various environmental variables and family species richness, we performed pairwise correlation analyses between them. For this analysis only, we controlled for the influence of family range-size on species richness by using contrasts in residuals from the regression of family species richness against area, rather than contrasting species richness directly. In all subsequent models we included contrasts in family range-size among the explanatory variables (see below).

To examine the relationship between diversification and environment, we explored four models. First, we tested if diversification varied with latitude by relating species

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richness contrasts to contrasts in family range-size and latitudinal position. Second, to explore the relative importance of past climate change and measures of energy availability, we fitted a model with species richness contrasts as the response, and mean annual temperature, seasonal variation in temperature, AET, mean elevation, standard deviation of elevation and mean annual temperature change between the present and the LGM according to one of the three GCMs, as explanatory variables. Third, we included latitude among the explanatory variables used above, to test whether our set of environmental variables could explain latitudinal variation in diversification. If latitude was retained as a significant predictor, it could indicate two things: either a variable closely correlated with latitude but not considered in

**Figure 1** Global pattern in richness of 172 flowering plant families. Family richness per grid cell was calculated by summing the number of families represented in each grid cell. Richness increases going from blue to red. Relative richness values correspond closely to those estimated by Francis & Currie (2003) based upon a wider sample of angiosperm families, indicating that the subset of families used in the present analysis provide a good surrogate for total angiosperm diversity.

**Figure 2** Absolute diversification rates of flowering plant families across the globe (excluding Antarctica) for all 172 plant sister families (centre) and for families divided into quartiles according to family range-size (43 families in each quartile) going from the families with the smallest (first quartile) to most widespread distribution (fourth quartile). Diversification rates were estimated for each family as ln(species number)/age of family, family range-size was then factored out by regressing diversification rate against range-size and plotting the geographical distribution of the residuals. Red indicates higher and blue lower diversification rates than predicted by range-size.
the present analyses was important for diversification, or latitude encapsulated environment across a family’s distribution better than our more direct measures. Fourth, we also included two-way interaction terms between the environmental variables in the regression models to explore non-additive effects. We used a model simplification procedure for the regressions, starting from a maximum model including all explanatory variables. Non-significant parameters were then removed in a stepwise fashion, following Crawley (2002), to produce a minimum adequate model.

RESULTS

Family richness (Fig. 1) of the 172 families peaked in tropical regions in general, a pattern also true for species richness (Davies et al. 2004b) and conforming to typical latitudinal patterns. In the first geographical map of global angiosperm diversification, we show that family diversification rates per grid cell, corrected for area, demonstrate substantial variation (Fig. 2). Diversification rates estimated using a birth-death model of diversification were virtually indistinguishable (data not shown). Surprisingly, tropical diversification rates were found to be comparatively low within the main blocks of tropical lowland rainforests (notably the Amazon and Congo basins and south-east Asia), where ecosystem productivity is highest. Rather, diversification rates were fastest in the Andes, Brazil’s Atlantic forests, tropical West Africa, Madagascar, north-western Australia, Mesoamerica and the Caribbean (Fig. 2).

Table 1 Multiple regressions between species richness and various combinations of explanatory variables

<table>
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<th>Model</th>
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Family range-size was included in all starting models. The environmental variables were mean annual temperature, seasonal variation in temperature, AET, mean elevation, standard deviation of elevation and climate change (mean annual temperature change between the present and the Last Glacial Maximum according to one of three GCMs: CCC2, ECHAM3 and UGAMP). Minimum adequate models after model simplification (Crawley 2002) are displayed for models 2–4. We report adjusted model $R^2$ to account for differences in the number of predictor variables between models.

AET, actual evapotranspiration; GCM, global circulation model.

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extratropical regions, including the Arctic and boreal regions of the Northern Hemisphere and inland Australia (Fig. 2). Dividing families into quartiles according to their rangesizes indicated that the apparently high diversification in the Arctic and boreal regions and in inland Australia was largely driven by families in the fourth quartile (those with the largest ranges). The geographic scale of the richness and diversification maps is arbitrary, we therefore also present lower resolution versions of Figs 1 and 2 (grain sizes $5^\circ \times 5^\circ$) for comparison as supplementary Figs S1 and S2.

Differences in species richness between sister families represent differences in relative rates of diversification, and were correlated with latitude even when range-size was controlled for (Table 1, model 1), supporting the hypothesis that the latitudinal gradient in flowering plant species richness can, in part, be explained by latitudinal variation in diversification rates. It is possible that some families may have been prone to over-splitting of species, inflating estimates of diversification rates and thereby biasing our results. However, this would most likely be the case for Northern Hemisphere families which have been more intensively studied, but we found higher rates in tropical families. Correlation analyses, summarized in Fig. 3, showed that temperature, AET and past climate change were intercorrelated ($r = 0.71$–$0.86$), varied latitudinally ($r = 0.79$–$0.95$) and correlated with species richness ($r = 0.28$–$0.35$), with greater species richness in regions of high temperature, high AET and small climatic oscillations. When fitting a regression model with all measures of the contemporary environment and climate change as explanatory variables, climate change was retained as the strongest predictor of species richness among the various environmental variables in the minimum adequate model, irrespective of the GCM from which climate change data were taken; direct measures of environmental energy dropped out during model simplification (Table 1, models 2a–c). Including latitude among the explanatory variables had a strong influence on which variables were retained in the minimum adequate models (Table 1, models 3a–c), suggesting model sensitivity to the set of starting variables. Latitude, temperature and AET were retained in all three minimum adequate models, and climate change was only retained in the model using climate change data from the CCC2 GCM (Table 1, model 3a). However, model check plots indicated that these models behaved poorly, and were disproportionately influenced by a few points of high leverage. Including two-way interaction terms between variables, but decreasing the stringency by which terms were retained in the model during model simplification (retaining terms only if the drop in residual deviance was $\geq 10\%$), resulted in climate change being retained along with range-size in two of the three minimum adequate models (CCC2 and UGAMP), whereas temperature and range-size were retained in the third (ECHAM3) (Table 1, models 4a–c).

**Figure 3** Correlation analyses between contrasts in family species richness, latitudinal position, actual evapotranspiration, climate change (temperature change between the present and the Last Glacial Maximum according to ECHAM3) and mean annual temperature after controlling for variation in family range-size. Values are Pearson correlation coefficients and are included to aid comparison between the various environmental variables. All statistical models reported in Table 1 were performed using least-squares regression through the origin (Methods).
Equivalent models for regressions unweighted for phylogenetic certainty are provided for comparison in Supplementary Table 1, and further emphasize model sensitivity. The unweighted models tended to favour seasonal temperature variation as the better predictor of species richness (Supplementary Table S1). Seasonality was not retained in any of the weighted models, however, additional correlation analyses (Supplementary Fig. S3) show seasonality co-varied with historical climate change more closely than with mean annual temperature. Therefore, it is possible that increased error, brought about by misspecification of sister families, made it difficult to detect the subtle differences in signal between seasonal and historical climatic change, especially given the relatively coarse scale of GCMs. It is also likely that the scale of the family distribution data contributed to the difficulty in differentiating unambiguously between contemporary and historical factors. However, further analysis exploring differences between only more narrowly distributed families supported our general conclusions, with the best fit model (lowest AIC) including only range-size and climate change as significant predictors (Supplementary Table S2).

Overall, past climate change could explain variation in species richness contrasts equally well compared to traditional measures of energy availability, such as temperature and AET, and this was consistent across all GCMs. However, there was large model sensitivity depending on the starting variables, which was most apparent when latitude was included among the explanatory variables. Evidently strong co-variation among the different variables likely further confounded attempts to distinguish between the relative influences of contemporary vs. historical measures. Nonetheless, climate change could explain up to 22% of the variation in species richness in the minimum adequate models. In contrast, the best of the contemporary measures, when retained in the minimum adequate model, explained typically < 10% (the single exception being temperature in model 4b which explained 19% of the variation). AET, frequently cited as one of the strongest predictors of regional angiosperm species richness (e.g. Francis & Currie 2003) was retained as a significant variable in only three (of nine) models, and explained 5–6% of the variation in species richness between sister families. This is an order of magnitude less than other studies focussing upon correlations with species richness rather than diversification rates. Further, the best model including climate change explained 9% more of the variation in species richness than the model favoured by Davies et al. (2004c).

**DISCUSSION**

We demonstrate a latitudinal gradient in diversification rates in flowering plants, and show that measures of past climate change can explain variation in diversification rates equally well compared to contemporary measures of energy availability, such as mean annual temperature or AET. In addition, the individual models explaining the greatest proportion of the variation in diversification included climate change as a key explanatory variable (Table 1). Our measures of climate change used estimates of global temperature increases from the LGM 21 ka to present. Can such recent change be representative of environmental conditions experienced by plant families since their origination, many of which diverged in the Cretaceous (Magallón et al. 1999; Wikström et al. 2001)? First, temperature change between the present and the LGM has been shown to be a good proxy for spatial patterns in climatic oscillations over the last millions of years, i.e. during the Pliocene and the Quaternary (Jansson 2003). Further, a latitudinal gradient in the amplitude of climatic oscillations would have been present throughout the history of Earth as a result of astronomical forcing of Earth’s orbit. Second, although splits between families are measured in millions of years, differences in species richness between sister families may have evolved at any time following divergence. Recent phylogenetic evidence indicates that diversification rates are highly labile (Davies et al. 2004a), and that much of present day species richness may have accumulated over short time-spans in rapidly diversifying lineages (e.g. see Klak et al. 2004; Kay et al. 2005; Hughes & Eastwood 2006).

**Correlates of diversity**

Our models explained around two-thirds of the variation in species richness between sister families. Range-size was always retained as the most significant predictor (Table 1), highlighting the necessity of correcting for area when evaluating species richness–environment relationships. The strong relationship between clade species richness and area has been demonstrated previously (e.g. Gaston & Blackburn 1997; Davies et al. 2004b, 2005). Clades occupying large geographic ranges might provide more opportunity for speciation, or rapidly speciating clades might diffuse across the landscape and therefore occupy a greater area (Rosenzweig 1995). The regression models marginally favoured climate change over contemporary energy as the better predictor of species richness, but were sensitive to the set of starting parameters (Table 1). Both energy measures and climate change varied latitudinally, and were intercorrelated (Fig. 3). Therefore, model sensitivity is perhaps not surprising, as the environmental variables accounted for similar spatial variation in the distribution of species richness. However, model sensitivity might also reflect the influence of both energetic and historical factors on diversification rates. Different strategies are therefore
required to determine the relative importance of contemporary vs. historical processes. One possibility would be to focus on exceptions to the latitudinal gradient, such as clades or areas with unusually high diversification at high latitudes, or cases of low diversification in low latitudinal positions (Jansson & Dynesius 2002). A second possibility is to evaluate the predictions made by each mechanism in turn, and contrast the relative weight of evidence in their support. Here, we focus on this latter approach. Data at finer spatial and taxonomic scales will be required to pursue the former approach, and should be the focus of future studies.

Most of the hypothesized mechanisms linking species richness to measures of energy availability (reviewed in Evans et al. 2005) can either be rejected or evidence is lacking for plants. Some mechanisms apply only to heterotrophic organisms and not plants. For example, more energy might translate into more trophic levels and greater abundance of rare resources that can be exploited by specialist species. Alternatively, more energy might lead to more biomass and hence more individuals, reducing the risk for extinction. However, in plants, the relationship between biomass and number of individuals is complex, being modular organisms. Critically, there is no evidence for an increase in the number of individuals in plant communities towards the equator (Currie et al. 2004). Other mechanisms are only valid under a particular set of conditions. For example, higher consumer pressure in energy-rich areas resulting in reduced competition, and thus enhancing plant coexistence, does not consider variation in length of food webs. Intensity of herbivory is a function of the number of trophic levels above consumers, and is thus not expected to exhibit a simple productivity gradient (Oksanen & Oksanen 2000). For a few mechanisms there is simply insufficient data to evaluate them, for example, faster recovery times from disturbance in high energy regions, reducing extinction risk by reducing the time at low population numbers. Finally, some hypotheses have already been tested and rejected, such as the faster-evolution hypothesis (Davies et al. 2004b). The only widely cited mechanism linking energy and species richness at continental to global scales that applies to plants and that has not been rejected or lacks evidence, proposes a link between water-energy dynamics, productivity and the number of viable niches (O’Brien 1998), for example, by allowing for more strata of vegetation, but it is not clear whether high resource availability should lead to high diversification. The interaction between environmental energy and water availability was represented by AET in our analysis. We found only a weak relationship between diversification and AET (Table 1), despite large variation in AET within latitudinal bands. We suggest water-energy dynamics might primarily affect coexistence of species and may thus be a better predictor of community species richness, reflecting species assembly from the regional species pool, rather than in situ diversification. Comparing our results with a comprehensive study investigating the environmental determinants of global patterns in plant species diversity (Kreft & Jetz 2007) is instructive. Whereas we found plant diversification to be most strongly related to climate change or temperature (Table 1), variation in plant species richness across the globe was best explained by a water-energy model (potential evapotranspiration and number of days with rain) along with habitat heterogeneity (topography and number of vegetation types) (Kreft & Jetz 2007).

We conclude that support for mechanisms relating energy availability to diversification rates is equivocal. In contrast, there is increasing evidence that diversification rates are modulated by climate change via orbitally forced range dynamics (ORD), i.e. changes in the geographical extent and location of species ranges in response to variation in the Earth’s orbit (Dynesius & Jansson 2000; Jansson & Dynesius 2002; Jansson 2003). Although ORD may favour the separation of gene pools in the short term, greater climatic fluctuations will tend to reduce net speciation rates by making it less likely that gene pools both remain isolated and survive until reproductive barriers evolve (Jansson & Dynesius 2002). Support for the role of ORD in shaping latitudinal gradients in species richness comes from several lines of evidence. First, there is a latitudinal gradient in ORD (Webb & Bartlein 1992; Bennett 1997). Second, in climatically more stable areas, gene pools are more finely spatially defined (Hewitt 2004; Hampe & Petit 2005; Grivet et al. 2006) and demonstrate greater genetic differentiation (Konner & Bergmann 1995; Hampe & Petit 2005). Finally, there is a negative correlation between the magnitude of climate change and number of endemic species of mammals, birds, reptiles, amphibians and vascular plants harboured in an area (Jansson 2003). In general, the larger the climatic shift, the more likely that palaeoendemics go extinct and/or the less likely that neoendemics evolve.

**Phylogenetic niche conservatism and tropical diversification**

We found that family richness was high in tropical regions in general (Fig. 1), but intra-tropical diversification rates were highly variable (Fig. 2). We therefore propose that high taxonomic richness in the lowland tropics can be explained by many families being restricted to tropical areas, and the long time of continuous existence of tropical rainforests, allowing lineages to accumulate over time (Fine & Ree 2006), consistent with the evolutionary time and tropical conservatism hypotheses (TCH; Fischer 1960; Wiens & Donoghue 2004), whereas high tropical richness...
outside the lowland rainforest may be better explained by rapid diversification. The six centres of high tropical diversification in Fig. 2 (the Andes, Brazil’s Atlantic forests, tropical west Africa, Madagascar, Mesoamerica and the Caribbean) are all classified as biodiversity hotspots (Myers et al. 2000), and include four of the five leading hotspots in terms of number of endemics (the Andes, Madagascar, Brazil’s Atlantic forests and the Caribbean; Myers et al. 2000), whilst the fifth hotspot of endemism (Sundaland) is also revealed to be a centre of rapid diversification when we consider only families falling into the first two range-size quartiles. Globally, areas with high endemic species richness have experienced little Quaternary climate change (Jansson 2003). For the Andes, the hotspot with the highest global share of endemic plants (Myers et al. 2000), low ORD has been implicated as the mechanism for high diversification rates due to the co-occurrence of paleoendemic and neoeconomic species (Fjeldså & Lovett 1997; Fjeldså & Rahbek 2006) and peaks in endemism in the climatically most stable mountain areas (Fjeldså et al. 1999; Fjeldså & Rahbek 2006). Although range dynamics have not been well documented for the other centres of diversification, they are characterized by proximity to oceans and/or presence of mountain ranges, which are associated with low ORD. Oceans tend to buffer climatic variability in adjacent land areas, and mountain sides allow populations to move only short distances in response to climatic change (van der Hammen 1995).

It remains possible that the diversification of species-rich clades occurred outside their current distributions. However, there are three lines of evidence supporting rapid diversification outside the lowland tropics: first, species level phylogenies reveal some of the most rapid recent diversification events outside these regions, such as the Andean genus Lupinus (Hughes & Eastwood 2006), South African ice plants (Aizoaceae; Klak et al. 2004) and the Hawaiian silversword alliance (Baldwin & Sanderson 1998). Second, centres of diversification are also centres of endemism as discussed above (Myers et al. 2000), suggesting in situ speciation. Third, there is evidence that bota in lowland tropics (e.g. plants and birds) represent old lineages, whereas recently diversified tropical taxa are found outside the main rainforest blocks, often in areas with concentrations of both novel and relictual taxa, suggesting active speciation owing to long-term stability in environmental conditions (Fjeldså & Lovett 1997).

Although we found relative diversification rates to be higher for more tropical clades (Table 1), absolute diversification rates were sometimes also high outside the tropics (Fig. 2). Are the results of the sister-group comparisons and the map of absolute diversification rates compatible? Some of the differences among the regions in the range-size quartile maps of Fig. 2 may simply reflect differences in average family range-size among regions. The unexpectedly high diversification rates observed in several high-latitude regions, notably the Arctic and boreal biomes, were driven by a few wide-ranging families, and hence might not be indicative of the true geographic distribution of diversification events, which may have occurred at any location within their range. This is even more likely when considering that the Arctic and boreal biomes have expanded in area during the late Tertiary and the Quaternary. Alternatively, it is possible that evolutionary turnover of species is faster at higher latitudes (Weir & Schluter 2007), and that apparent high net diversification rates across these latitudes are a product of recent speciation events within relatively young families, but that high extinction rates maintain low standing diversity. If the latter were the case, extinction and not speciation, might be the major driver of latitudinal gradients. Future analyses at a finer spatial scale using more recently diverged sister-groups, for which the environmental conditions they have experienced and the location of divergence events are better known, will be required to explore this further.

**CONCLUSIONS AND PERSPECTIVE**

We have shown that (i) diversification rates increase towards the equator, suggesting that the latitudinal diversity gradient can, in part, be explained by differences in diversification rather than simply post-speciation migration, (ii) orbitally forced climatic oscillations can explain variation in diversification equally well compared to measures of energy availability and (iii) diversification rates in the tropics are faster for clades currently found within endemic-rich regions outside the main blocks of tropical lowland rainforest. We conclude that lowland tropical clades may be more species rich because of low extinction rates and the gradual accumulation of diversity, made possible by long periods of environmental stability, whereas absolute diversification rates are higher in areas characterized by concentrations of endemic species and low ORD, such as the Andes. Orbitally forced range dynamics (Dynesius & Jansson 2000) and the TCH (Wiens & Donoghue 2004) offer unique predictions, and both likely contribute to the latitudinal gradient in plant diversity. The fact that lower-latitude families that have experienced lower amplitude of climatic oscillations have accumulated more species than their higher-latitude sister families from more climatically dynamic areas suggest a role for ORD independent of the TCH, since sister families originated at the same time. In contrast, the high number of tropical families, and the accumulation of species over time in tropical lowland rainforests (as suggested by high richness and low diversification rates) are patterns predicted by the TCH.
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REFERENCES


**SUPPLEMENTARY MATERIAL**

The following supplementary material is available for this article:

**Figure S1** Global pattern in richness of 172 flowering plant families displayed at 5°x5° resolution.

**Figure S2** Absolute diversification rates of flowering plant families across the globe displayed at 5°x5° resolution.

**Figure S3** Correlation analyses between contrasts in seasonality (seasonal variation in temperature), mean annual temperature and climate change.

**Figure S4** Frequency histogram of family range sizes.

**Table S1** Multiple regressions between species richness and various combinations of explanatory variables using unweighted contrasts.

**Table S2** Multiple regressions between species richness and various combinations of explanatory variables as for Table 1 in the main text, but including only contrasts between more narrowly distributed families.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2007.01138.x

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