

Environmental causes for plant biodiversity gradients

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One of the most pervasive patterns observed in biodiversity studies is the tendency for species richness to decline towards the poles. One possible explanation is that high levels of environmental energy promote higher species richness nearer the equator. Energy input may set a limit to the number of species that can coexist in an area or alternatively may influence evolutionary rates. Within flowering plants (angiosperms), families exposed to a high energy load tend to be both more species rich and possess faster evolutionary rates, although there is no evidence that one drives the other. Specific environmental effects are likely to vary among lineages, reflecting the interaction between biological traits and environmental conditions in which they are found. One example of this is demonstrated by the high species richness of the iris family (Iridaceae) in the Cape of South Africa, a likely product of biological traits associated with reproductive isolation and the steep ecological and climatic gradients of the region. Within any set of conditions some lineages will tend to be favoured over others; however, the identity of these lineages will fluctuate with a changing environment, explaining the highly labile nature of diversification rates observed among major lineages of flowering plants.

Keywords: species richness; evolutionary rates; environmental energy; biological traits; angiosperms

1. INTRODUCTION

The major biomes span the diversity of life across the Earth, ranging from the high species richness found within the wet tropics to the virtually lifeless polar deserts. Fundamentally, species richness is a product of speciation minus extinction (Godfray & Lawton 2001), hence, understanding how these factors vary across the Earth will be an important element in unraveling biome history. The search for a primary cause of the uneven distribution of species richness and, in particular, the widely cited decrease in diversity from equator to poles, has posed a challenge to biologists for over a century (Hawkins 2001). However, the clumped nature of species richness has important implications for prioritizing conservation efforts (Myers *et al.* 2000) and in interpreting evolutionary processes driving diversification within continental biomes.

The trend for species richness to decline at higher latitudes has been documented for a wide range of taxa (e.g. woody plants: Currie & Paquin 1987; birds and butterflies: Cardillo 1999; marine fishes and invertebrates: Rex *et al.* 1993; Macpherson 2002). Although not universal (e.g. Valdovinos *et al.* 2003; and see Gaston *et al.* 1998; Willig *et al.* 2003) and more pronounced in the Northern Hemisphere than the Southern Hemisphere (Platnick 1991), the

latitudinal gradient in species richness remains one of the most ubiquitous patterns in ecology, the pervasiveness of which is indicative of a common cause (Pianka 1966; Rohde 1992). Similar gradients in diversity have been found in the spatial distribution of higher taxonomic groups (e.g. genera: Qian & Ricklefs 2000; and families: Gaston *et al.* 1995) and within the fossil record (Stehli *et al.* 1969), implying that underlying causal mechanisms span an evolutionary time-scale. We outline how phylogenetic analyses can enhance our understanding of the broad effects of the environment on evolutionary rates and diversification in flowering plants (angiosperms), focusing on latitudinal gradients and the role of environmental energy.

2. HYPOTHESES EXPLAINING THE LATITUDINAL GRADIENT IN SPECIES RICHNESS

Despite many putative hypotheses about the latitudinal gradient in species richness (Rahbek & Graves (2001) suggested over 100), they have concentrated largely upon ecological explanations (Rosenzweig 1992; Gaston & Williams 1996; Francis & Currie 2003; Willig *et al.* 2003). Some, such as increased competition at low latitudes (Pianka 1966) or environmental harshness at high latitudes (Whittaker 1965), have been criticized as circular because it is either difficult to distinguish between cause and effect or define the parameters without referring back to species richness itself (Rohde 1992). Others, such as aridity or host diversity, are too specific to be able to account for global patterns (Willig *et al.* 2003).

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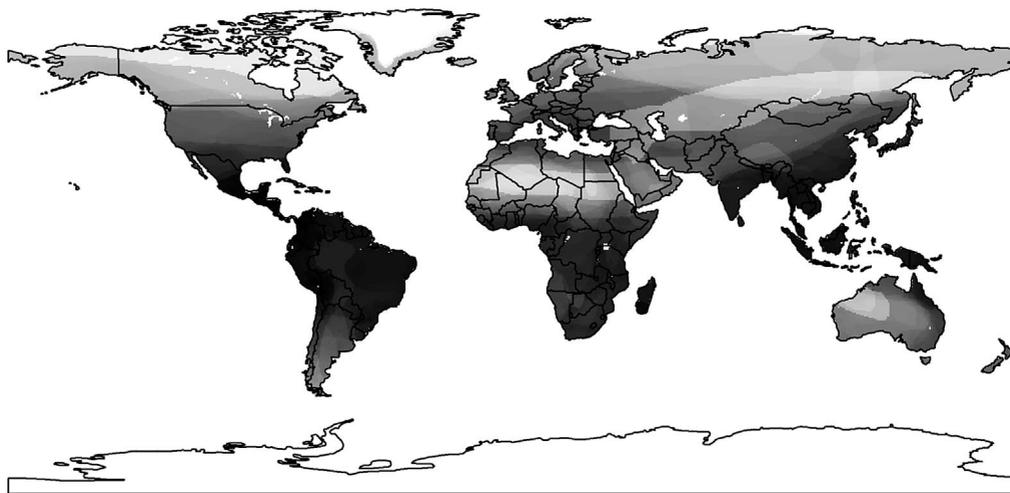


Figure 1. Angiosperm species richness estimated from overlaying family distribution maps from Davies *et al.* (2004b), representing 172 families. Species richness varies from low (light) to high (dark).

One dominant explanation has been that geographical range size or available area might vary with latitude. For example, Rapoport's rule states that seasonal variation at high latitudes favours species with broad ecological tolerances and therefore wide (latitudinal) ranges (Stevens 1989). The lower ecological tolerance of species in the tropics may therefore result in greater effective spatial heterogeneity at lower latitudes and lead to denser species packing. These geographically limited populations may also be more likely to disperse into nearby but unsuitable (sink) habitats, further inflating local species richness (the Rapoport-rescue effect). Alternatively, it has been argued that the greater surface area of climatically similar environments enables species in the tropics to have greater range sizes (Rosenzweig 1992). First, this may result in an increased overlap of species distributions at lower latitudes. Second, greater geographical area may support greater population sizes and potentially an increase in the number of refugia within a species' range, thereby reducing extinction risk. Third, the probability of major barriers reproductively isolating populations might be greater for species with large ranges, thereby elevating rates of allopatric speciation. Thus, area may place an upper limit on diversification of a given clade (Owens *et al.* 1999; Ricklefs 2003), whereas taxa encompassing small ranges may be unlikely to diversify at all (Losos & Schluter 2000).

Another dominant hypothesis has been that high levels of environmental energy promote species richness (e.g. amphibians: Currie 1991; angiosperms: Wylie & Currie 1993; birds: Turner *et al.* 1988; Currie 1991; Wylie & Currie 1993; insects: Kerr 1999; mammals: Currie, 1991; Kerr 1999; marine fauna: Macpherson 2002; reptiles: Currie 1991; and trees: Currie & Paquin 1987; O'Brien 1993). The two principal explanations to the observed relationship between species richness and energy are as follows.

- (i) The biomass–energy hypothesis (Wright 1983). Greater energy availability at lower latitudes may support a greater biomass and hence more populations (rather than simply more individuals per population).
- (ii) The faster-evolution hypothesis (Rohde 1992). Environmental energy may speed up evolutionary

rates and species production; the high energy load of tropical regions may increase metabolic rates and/or decrease development times leading to shorter generation times, faster mutation rates and, as a consequence, increased net diversification rates. The increasing availability of detailed phylogenetic data, providing information on the evolutionary history among a subset of the branches from the tree of life, offers the potential to investigate such evolutionary explanations to the latitudinal gradient.

If the faster-evolution hypothesis is correct, species richness might be expected to be correlated with the rate of molecular substitution, reflecting evolutionary rates—the evolutionary clock is ticking faster in these lineages. Sister-family contrasts among angiosperms performed by Barraclough *et al.* (1996), Savolainen & Goudet (1998) and Barraclough & Savolainen (2001) found that species-rich families do tend to be characterized by faster rates of molecular evolution and that this correlation was strongest for neutral substitution rates, as would be predicted if general evolutionary rates rather than selection pressure were influencing diversification rates. We review the evidence that environmental energy drives diversification rates within angiosperms and assess the importance of the interaction between biological traits and environment.

3. FLOWERING PLANTS

The distribution of angiosperm species richness follows a typical latitudinal gradient, the most noticeable exception being Saharan Africa (figure 1), with many fewer species than areas of similar latitude. Fossil evidence indicates a palaeotropical origin, whence they radiated to higher latitudes over the next 20–30 Myr (Crane & Lidgard 1989; Drinnan *et al.* 1994; Lupia *et al.* 1999), accompanied by a rapid rise to ecological dominance between 100 and 70 Myr ago (Barrett & Willis 2001). Analyses of the taxonomic distribution of species richness among angiosperms show a considerable skew in the frequency distribution of the imbalance of sister taxa, with a large dis-

parity in the number of species between closely related lineages (Dial & Marzluff 1989; Fusco & Cronk 1995; Davies *et al.* 2004a). This imbalance is much greater than that expected by chance if all taxa had an equal probability of diversifying and is characteristic of the general pattern found across a wide range of taxa (Marzluff & Dial 1991; Purvis 1996; Savolainen *et al.* 2002). One possible explanation for rejection of the equal-rates model is the evolution of novel traits that influenced diversification rates (Purvis 1996). A great deal of work has focused on the importance of key innovations in influencing net speciation rates among lineages (e.g. Slowinski & Guyer 1989; Marzluff & Dial 1991; Guyer & Slowinski 1993; Heard 1996), and several traits within angiosperms have attracted particular attention.

- (i) Generation time, associated with either life form (herbaceous versus woody) or habit (annual versus perennial), may influence the rate of evolution (Eriksson & Bremer 1992; Gaut *et al.* 1992, 1996; Andreasen & Baldwin 2001), and species characterized by short generation times with a high intrinsic rate of population increase may also be more robust to extinction, further influencing net diversification rates.
- (ii) Monoecy may be correlated with increased probability of speciation after hybridization (Rieseberg 1997) or long-distance dispersal (Baker 1955), whereas the tendency for dioecious species to have generalist pollinators may inhibit reproductive isolation necessary for speciation (Bawa & Opler 1975; Bawa 1994).
- (iii) Biotic pollination might increase reproductive isolation through pollinator specificity (Grant 1949) and has been implicated as instrumental in the rapid diversification of orchids around the late Cretaceous (Crane *et al.* 1995).
- (iv) Biotic dispersal might increase the probability of long-distance dispersal, promoting establishment of isolated populations, which may then diverge (Eriksson & Bremer 1992).

Until recently, our understanding of the evolutionary history of angiosperms was hampered by insufficient phylogenetic knowledge, and analyses of character evolution hinged upon the alternative phylogenetic resolutions adopted (Doyle & Donoghue 1993; Sanderson & Donoghue 1994; Friedman & Floyd 2001). The revolution in molecular techniques and development of phylogenetic theory during the 1990s enabled the production of a draft phylogenetic tree for all flowering plants (Chase *et al.* 1993; also see Chase & Albert 1998). The Angiosperm Phylogeny Group (APG 1998, 2003) produced the first framework for coordinated systematic data collection within one of the major taxonomic groups, the flowering plants, and studies containing more than 100 taxa based on molecular characters are now commonplace (Savolainen & Chase 2003). Despite this increasing wealth of phylogenetic data, evidence for key innovations affecting diversification rate among higher angiosperm clades remains inconclusive (Salamini & Davies 2004).

The supertree of Davies *et al.* (2004) provided the first comprehensive estimate of phylogenetic relationships among all angiosperm families, allowing broad-scale patterns of diversification to be examined. By calibrating branches of the tree from the fossil record, Davies *et al.*

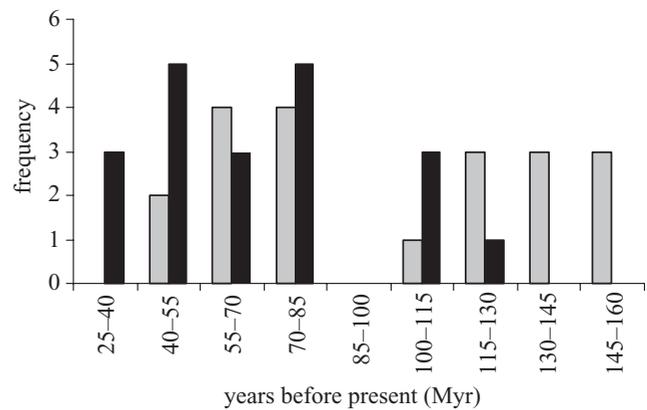


Figure 2. Frequency histogram of the 20 most evenly balanced nodes (black bars) in terms of species richness using the method of Slowinski & Guyer (1993) and the 20 most imbalanced nodes (grey bars), from Davies *et al.* (2004a), excluding nodes that collapsed in the strict consensus tree, distributed among nine 15 Myr time-windows.

(2004a) demonstrated that absolute diversification rates varied considerably among clades and over geological time. A large proportion of the clades at nodes deeper in the phylogenetic tree tend to be highly imbalanced in terms of species richness, whereas many of the most balanced clades are at more recent nodes (figure 2). The greater imbalance of older nodes may reflect the accumulated effect of selective sweeps, brought about by environmental change, upon extinction and/or speciation rates in the respective clades.

A comparison of absolute diversification rates by Magallón & Sanderson (2001) revealed several lineages with many more species than predicted (e.g. Lamiales, Asterales, Fabales, and Poales), whereas others were much less species rich than expected (e.g. Buxaceae, Platanaceae, Typhaceae and Nymphaeaceae). The former are over represented among euasterids and the latter among more early diverging lineages, indicating a heritable component to the probability of diversification, but the overall pattern is one in which the propensity to diversify is highly labile. Both lineages with high and low net diversification rates are distributed among all major angiosperm clades, and there is a growing appreciation that explanations based upon one or a few traits are too simplistic (Sanderson & Donoghue 1994; Magallón & Sanderson 2001; Sims & McConway 2003; Davies *et al.* 2004a).

4. ENVIRONMENTAL CORRELATES OF EVOLUTIONARY RATES

If environmental energy were driving diversification rates it would be expected that lineages experiencing a higher energy load would contain more species. Davies *et al.* (2004b) evaluated this contention by performing independent contrasts between sister-family pairs from the phylogenetic tree of Soltis *et al.* (1999, 2000). This phylogenetic tree encompassed *ca.* 75% of angiosperm families and sampled nuclear ribosomal and plastid DNA, providing one of the best-supported molecular phylogenetic estimates of the group. As, by definition, sister taxa are of the same age, any difference in species richness or molecular branch lengths must reflect variation in rates.

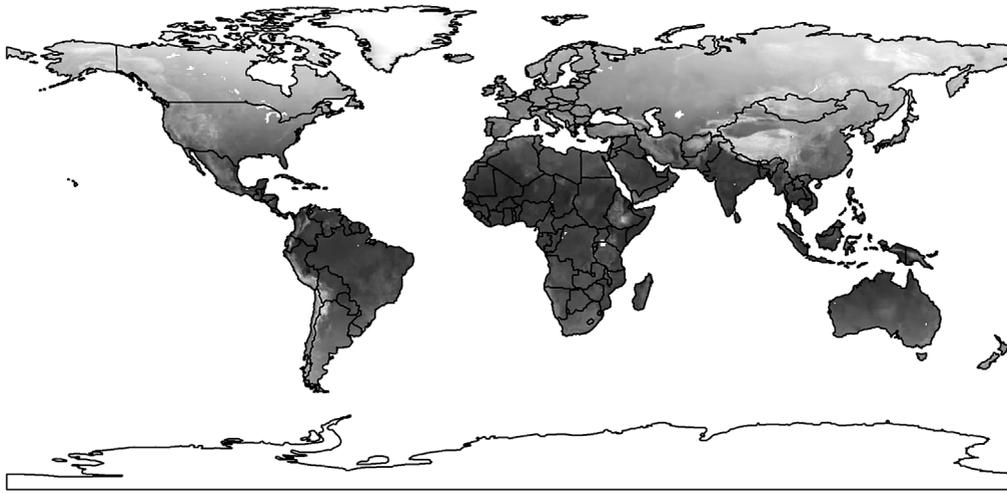


Figure 3. Average surface air temperature obtained from the online Global Ecosystem Database (http://www.ngdc.noaa.gov/seg/eeco/cdroms/gedii_a/datasets/a03/lc.htm), between 1931 and 1960, from low (light) to high (dark).

Energy load across contemporary distributions of angiosperm families was estimated from GIS data. Three direct measures of energy were examined; AET, UV and temperature, along with three confounding factors: area, elevation and latitude.

- (i) AET is the quantity of water that is actually removed from a surface due to the processes of evaporation and transpiration, an index of the potential biomass an area can support. AET is typically high in the wet tropics and low in arid environments and towards the poles as temperature decreases. If the biomass–energy theory were correct we may expect that AET would demonstrate the strongest correlation with species richness.
- (ii) UV load was measured in terms of erythemal exposure, an estimate of the potential for biological damage due to solar irradiation (Herman & Celarier 1999). UV has been associated with several mutagenic pathways through the production of harmful photoproducts (Jansen *et al.* 1998; Rozema *et al.* 1997) and has been described as a ‘driving force in evolutionary rates’ (Rothschild 1999), but it appears to have little direct influence on primary productivity or biomass (Caldwell *et al.* 1995). It has been proposed that the unusually long molecular branch lengths subtending some planktonic foraminifera, an indication of high rates of molecular change, were a result of high UV exposure in the photic zone (Pawłowski *et al.* 1997).
- (iii) Temperature. Both biomass and mutation rates might be affected by ambient temperature, either through decreasing development times or increasing metabolic rate and production of DNA-damaging metabolites (Allen *et al.* 2002). Although no correlation between metabolic rate and mutation rates was found within mammals (Bromham *et al.* 1996), the link may be stronger for ectotherms (Allen *et al.* 2002). If the faster-evolution theory were correct, it might be expected that UV and/or temperature would display the strongest relationship with species richness, through an intermediate link with molecular rates.

The accuracy with which contemporary estimates can reflect energy load experienced over evolutionary time is dependent upon both range movement and climatic change. Although it is known that climatic shifts occur in the order of every 10 000–100 000 years, e.g. those brought about by Milankovitch oscillations (Dynesius & Jansson 2000), the average age of a family is *ca.* 60 Myr (Wikström *et al.* 2001), and hence even the youngest families are likely to have experienced several changes in climate since the time of divergence from their nearest relative. However, a migration-like response to climate change, with species distributions tracking environmental conditions, is well documented (Huntley & Webb 1989), and hence mean energy load may be relatively constant over time. Therefore, contemporary distributions may be able to provide meaningful estimates of energy load; if this were not the case, it would most probably confound attempts to detect any relationship between evolutionary rates and environmental correlates.

Contrasts in the log number of species and the mean energy load experienced across family distributions were calculated for each sister pair together with the difference in the lengths of the molecular branch lengths subtending the respective taxa, representing relative molecular rates. The relationship between species richness, environmental energy and molecular rates was explored by constructing a series of models using least-squares regression through the origin (Harvey & Pagel 1991). Model simplification was then performed to obtain a minimum adequate model for each analysis (see Appendix A for further details). Results of Davies *et al.* (2004b) can be summarized as follows.

- (i) Species richness. All measures of environmental energy were strongly correlated with species richness. Area was the single best predictor of species richness with temperature the most predictive of the energy measures (compare figure 1 with figure 3), although the alternative measures of energy performed almost as well.
- (ii) Molecular rates. As predicted by the faster evolution theory, rates of molecular evolution were also strongly correlated to environmental energy, this time with latitude retained as the single best predictor. The

relationship was consistent across both nuclear and plastid regions and protein-coding and ribosomal genes, reflecting the influence of environmental energy on general evolutionary rates.

- (iii) The faster-evolution theory. If environmental energy were driving diversification rates by its effect on rates of molecular evolution, molecular rates would be the more immediate predictor of species richness. However, when both molecular rates and environmental energy were included as explanatory variables, with species richness as the response, molecular rates were removed during model simplification, leaving energy as the more immediate predictor variable. The correlation between molecular rates and species richness found in previous studies (Barracough & Savolainen 2001; Webster *et al.* 2003) is probably a result of the confounding effect of environmental energy.

Wright (1983) argued that area itself had no direct effect, but rather represented an indirect measure of resource availability or energy. However, area was retained as the most significant predictor of species richness after inclusion of more direct estimates of energy load as explanatory variables, and hence area is unlikely to be simply a surrogate for available energy. The relationship between species richness (S) and area (A) is commonly represented by the power law function $S = cA^z$, where c and z are constants, the latter varying at different spatial scales (Crawley & Harral 2001). For angiosperm families used in the analysis z was 0.44 (0.51 for the sister contrasts), although the large variance in geographical distributions among families is likely to have encompassed a range of spatial scales, in which different processes may be dominant (see Losos & Schluter 2000). So far, the relationship between geographical area and species richness among lineages has not been rigorously evaluated. Whether geographical area is a function of species richness or species richness a function of area is not immediately clear. Species-rich clades may encompass a greater geographical range as lineages radiate out from a central point of origin following speciation events. Alternatively, lineages with large geographical ranges may have higher net diversification rates (see § 2 above).

A correlation between environmental energy and molecular rates has not been demonstrated among any other group (Bromham & Cardillo 2003). The relationship holds across both rates of neutral and functional changes and is consistent with a shortening of generation times or elevated mutation rates in high-energy environments. However, there is no evidence that molecular rates are an intermediate step between environmental energy and species richness, but rather the effect of the environment upon species richness is direct, and thus the faster evolution theory was not supported.

The inability to differentiate between alternative energy measures may, in part, be a consequence of the taxonomic scale of the analysis. Although use of independent contrasts reduces the effect of confounding variables (Barracough *et al.* 1998), clades at nodes deep in the phylogenetic tree are still likely to differ in many aspects, not only geographical distribution, and the errors surrounding the use of contemporary measures as a surrogate for those experienced over evolutionary time will be greater for older

nodes. Analysis at a finer taxonomic scale may be able to provide sufficient resolution to discriminate among the measures, although until a more comprehensive phylogenetic analysis of the angiosperms is produced, i.e. complete sampling at the genus level, increased taxonomic resolution will come at the sacrifice of generality.

5. INTERACTION BETWEEN BIOLOGICAL TRAITS AND THE ENVIRONMENT

The importance of particular traits in influencing patterns of diversification is likely to be contingent upon the possession of other traits and environmental conditions (de Queiroz 2002), and, by corollary, the influence of the environment on diversification rates will be dependent upon the biological traits of the taxa in that environment. Species-rich and species-poor clades may therefore share traits associated with increased rates of cladogenesis, but the potential to diversify is conditional upon additional circumstances such as geographical area, favourable habitats or additional traits required for specific habitats. With a changing environment, different traits might have been advantageous at different geological times, with those taxa that happened to be pre-adapted to changes in environmental conditions rapidly diversifying. Such a scenario has been suggested to explain the rapid radiation of grasses coinciding with the late Tertiary change towards a drier climate (Axelrod 1952; Chapman 1996).

Contemporary species richness may therefore be largely a product of recent diversification events reflecting current environmental conditions, a conjecture supported by the weakly negative correlation between family age and species richness (Burger 1981; Salamin & Davies 2004). Hence, contrasts in species richness at deeper nodes (i.e. among older lineages) may be incapable of resolving the complex interaction between biological traits and the environment. To investigate more recent diversification events, T. J. Davies, V. Savolainen, M. W. Chase, P. Goldblatt and T. G. Barracough (unpublished data) performed species richness contrasts for a generic-level phylogenetic tree of Iridaceae.

Iridaceae are among the most species-rich monocot families, with a global distribution favouring dry Mediterranean climates; they are especially diverse in South Africa, eastern Mediterranean, and Central and South America, coinciding with biodiversity hotspots of the Cape of South Africa, succulent Karoo, tropical Andes and Mesoamerica identified by Myers *et al.* (2000). Among these areas the Cape, referring to the geographical area characterized by a Mediterranean climate and defined by the Cape Folded Mountain Belt, is remarkable for its high proportion of endemics, comprising *ca.* 80% of the approximately 677 Iridaceae species indigenous to the region (Goldblatt & Manning 2002). Defining features of the family include a predominantly herbaceous growth form, underground storage organs in the form of corms, rhizomes or bulbs and an isobilateral leaf held vertically. Floral morphology is highly variable but characterized by the unique possession of three stamens and an inferior ovary (Goldblatt 1990).

Using generic distribution maps, T. J. Davies, V. Savolainen, M. W. Chase, P. Goldblatt and T. G. Barracough (unpublished data) re-evaluated the relationships between

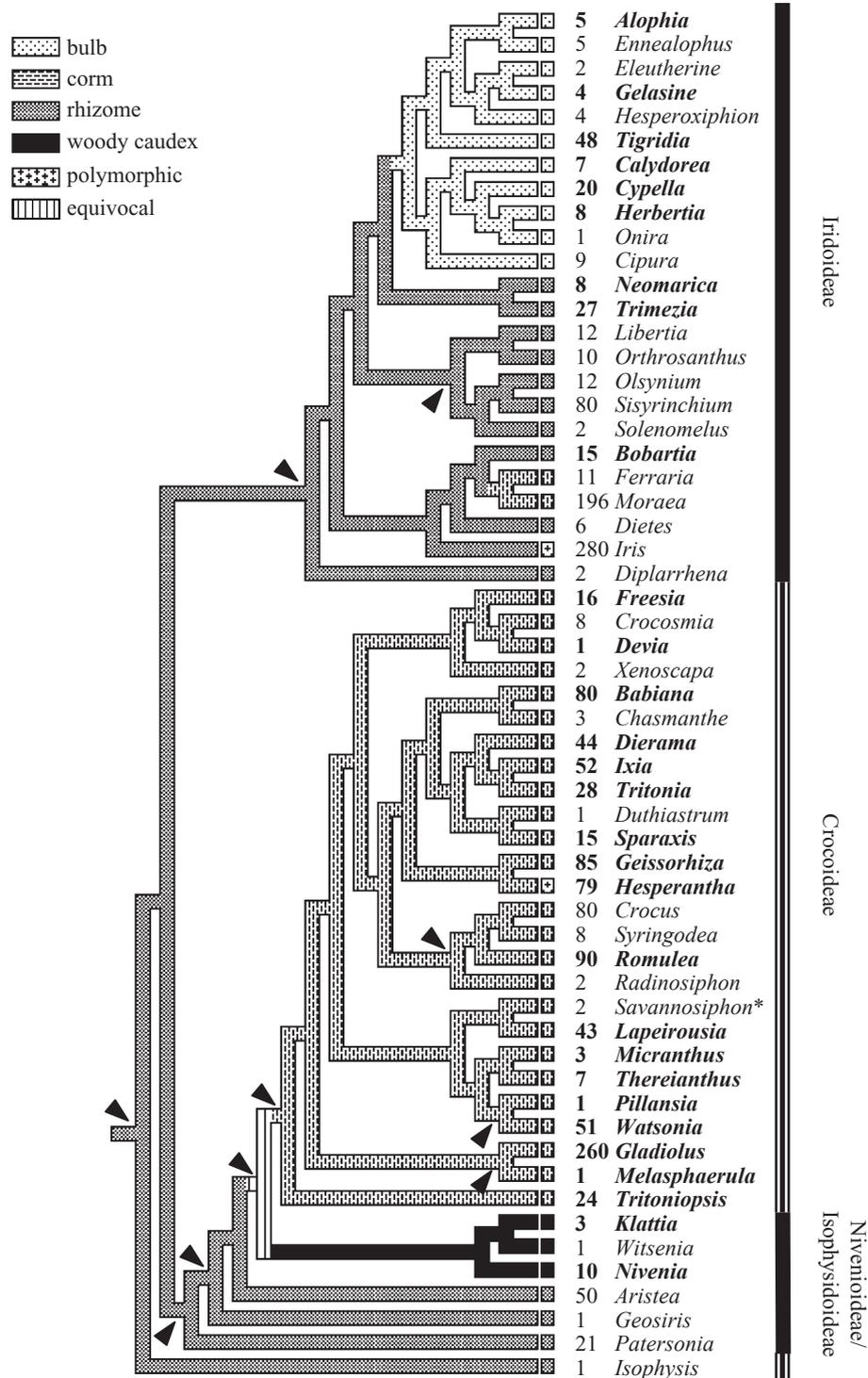


Figure 4. One of the two most parsimonious phylogenetic trees of Iridaceae (Davies 2004; P. Goldblatt, T. J. Davies, J. Manning, M. van der Bank and V. Savolainen, unpublished data) depicting the relationships among 57 genera and an ancestral reconstruction of root stem type. Arrowheads indicate nodes subtending sister clades that differ significantly in species richness, using the imbalance measure of Slowinski & Guyer (1993). Taxon names in bold indicate genera containing more species than predicted from environmental variables alone. Figures preceding taxon names are species richness values for the respective genera. * *Savannosiphon* includes *Cyanixia*.

environmental energy and species richness (see Appendix B for further details). Contrary to the strong positive correlation between energy and species richness found among angiosperm families, species richness within Iridaceae is negatively correlated to both UV and AET, whereas latitude and elevation show a positive correlation. Unlike alternative energy measures, temperature remains

positively correlated with species richness. The strong positive association between geographical area and species richness is retained, re-enforcing the importance of including area when examining environmental correlates of diversification rates. These findings may reflect more the specific habitat preferences of the family than a general effect of energy load upon net diversification rates. Neither

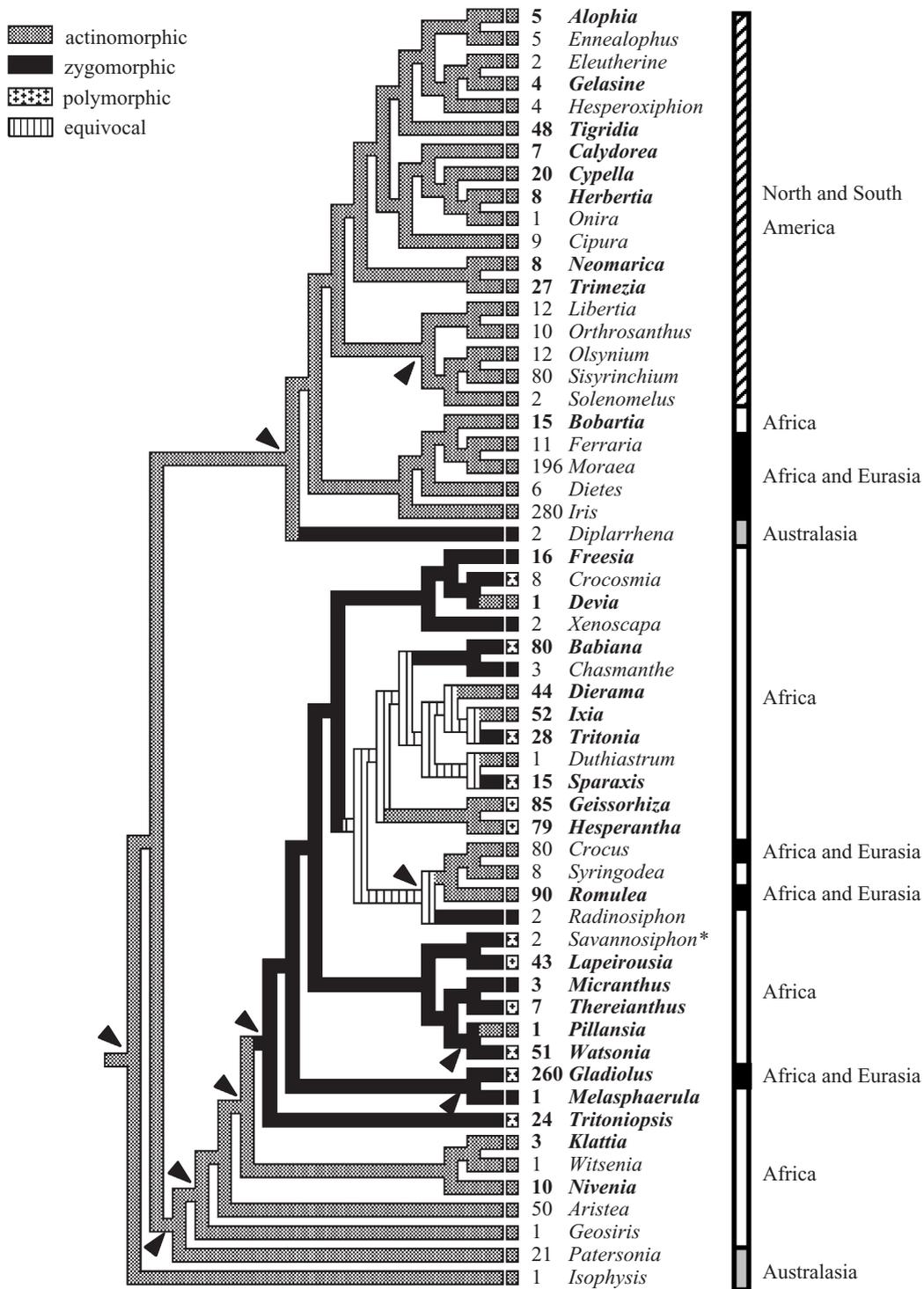


Figure 5. Phylogenetic tree topologically identical to that in figure 4, with ancestral reconstruction of flower symmetry, actinomorphic = radial symmetry, zygomorphic = bilateral symmetry. Genera are coded to reflect most species within the clade; if secondary reversals have occurred this is indicated as a polymorphism at the terminal, but this was not considered in the trait reconstruction. Continental distributions are given for the higher clades; all other annotations are equivalent to those in figure 4.

the biomass-energy nor faster-evolution theories are supported within Iridaceae by these results.

The negative correlation with AET indicates a relatively low productivity environment characterized by a warm climate and a topographically diverse habitat (positive correlation with temperature and elevation, respectively). Although a few genera are recorded from the Neotropics, for example *Neomarica* and *Eleutherine*, many of the traits

associated with intense competition for light or gap colonization, characteristic of species from the wet tropics, are not typical of Iridaceae. Instead, unusually species-rich genera are characterized by a cormous habit, highly varied floral morphology, a diverse array of pollination mechanisms and short dispersal distances, for example *Geissorhiza*, *Hesperantha*, *Ixia* and *Thereianthus*.

Large shifts in net diversification rates can be observed at the base of both the Crocoideae and Iridoideae clades (figure 4); however, these appear to be more closely associated with a geographical expansion into Africa and America from an Australasian origin rather than tied to the evolution of particular sets of biological traits. Furthermore, several of the traits characteristic of species-rich genera are also possessed by several genera with less species than predicted from climatic conditions, e.g. *Iris* and *Olsynium*. To further explore the relationship between biological traits and residual variation in species richness (that unexplained by the environmental variables included within the analysis) we use parsimony to reconstruct ancestral states in MACCLADE v. 4.06 (Maddison & Maddison 2003) for two morphological traits proposed to have been key to the success of the group: root type (figure 4) and floral symmetry (figure 5). Underground storage organs were probably important in the ability to colonize seasonally dry and fire dominated habitats (Goldblatt & Manning 2002; Linder 2003). The evolution of floral complexity associated with a bilaterally symmetrical flower (floral zygomorphy) may have allowed pollinator specificity and enhanced reproductive isolation between incipient species (Goldblatt 1991; Bernhardt & Goldblatt 2000).

Figures 4 and 5 reveal that neither root type nor flower symmetry are unambiguously correlated with either the large shifts in net diversification rate reconstructed on the phylogenetic tree nor with residual variation in species richness. Crocoideae are characterized by a cormous root stem but within this clade we see several shifts in diversification rates, indicated by imbalanced nodes (figure 4). Some genera are cormous and have more species than predicted (from environmental variables), whereas others are cormous but have fewer species than predicted. Floral symmetry is revealed to be a highly labile trait within Crocoideae and surprisingly demonstrates several reversals from the supposedly more derived zygomorphic state to actinomorphy. However, the positive association between floral zygomorphy and species richness reported among angiosperm families by Sargent (2004) is not strongly supported in Iridaceae. Hence, we find that, within the context of the characters examined, biological traits alone or in conjunction with broad environmental variables can only partly explain the disparity in species richness between clades.

A projection of the spatial distribution of residual variation in species richness displays a distinct geographical pattern, with southern Africa, and in particular the Cape, having many more species than regions of equivalent climate. The unusually high species richness of the region has long been recognized (e.g. Takhtajan 1986). Although it is argued that the high levels of endemism within the Cape are restricted largely to the species level because much of the diversity at higher taxonomic levels is also represented in adjacent parts of southern Africa (Cox 2001), regional diversity in the Cape ranks among the highest in the world (Cowling *et al.* 1996; Goldblatt & Manning 2002).

General climate–energy models tend to under-predict the high diversity found within the Cape (O'Brien *et al.* 2000; Taplin & Lovett 2003). Among a large number of hypotheses (see Cowling *et al.* 1996; Goldblatt & Manning 2002), the high frequency of rare endemics within the Cape indicates that the high species richness of the region is, at

least partly, a product of rapidly speciating lineages (Cowling *et al.* 1992). The combination of biological traits associated with limited dispersal and pollinator specificity characteristic of Iridaceae, allowing rapid reproductive isolation (Goldblatt 1991), with the highly heterogeneous environment of the Cape, may have been key to the rapid diversification of the family within the region. The disparity in diversification rates among genera of Iridaceae is therefore a likely product of both their specific biological traits and the environments in which they are found. A greater sample size of lineages would allow this hypothesis to be evaluated directly.

6. CONCLUSION

Environmental energy can explain a significant proportion of the variation in species richness among angiosperm families. Despite finding that rates of molecular evolution also tend to be higher in energy-rich environments, there is no evidence in support of the faster evolution hypothesis, in which energy drives diversification through an intermediary effect on evolutionary rates. Instead the main effects of environmental energy on both species richness and molecular rates are direct and more consistent with the energy-biomass theory; either speciation rates are faster or extinction rates are lower in regions supporting greater biomass. Our interpretation of the species–energy relationship is dependent upon the accuracy with which contemporary distributions reflect conditions experienced over evolutionary time; however, the observed correlation between contemporary energy load and evolutionary rates would remain.

Out of the energy measures, temperature was the single best predictor of species richness; however, the alternative measures perform almost as well. Phylogenetic information at a finer taxonomic scale may enable the significance of the alternative measures of energy to be evaluated. One possibility would be to concentrate attention on clades that differ in their relative exposure to the respective measures. Alternatively, predictions obtained from contemporary measures could be compared to models derived from palaeoclimatic data (see Stokstad 2001), using evidence from the fossil record to assess the accuracy of inferred ancestral distributions (see Swenson *et al.* 2000). A high degree of uncertainty is attached to both approaches; however, a close match between them would provide valuable corroborative support.

Whichever measures prove most important, environmental energy provides an evolutionary explanation to the latitudinal gradient in species richness. The biomass theory offers a plausible mechanism by which energy-rich regions have higher net rates of diversification. Some of the predictions of the biomass theory may be evaluated using current data; for example, abundance should be correlated with species richness. However, whether accumulation of species richness is a product of reduced extinction risk or rapid speciation may be harder to ascertain. If high net diversification rates were a product of reduced extinction risk, species-rich clades may be characterized by a high proportion of old lineages (Nee *et al.* 1994; Pybus & Harvey 2000). Alternatively, if species richness were a product of rapid speciation among taxa with large range

sizes, species-rich clades may be more likely to be characterized by many young lineages.

The pattern of species richness among genera of Iridaceae is inconsistent with the species–energy relationships found across angiosperm families. Instead, they reflect more the habitat preferences of the family and illustrate that the effect of the environment is likely to vary among lineages depending on their specific traits and specific features of regions they inhabit. The phylogenetic tree of the angiosperms is too imbalanced to be a product of an equal-rates Markov process, but shifts in diversification rate appear to be too frequent for it to be explained by the inheritance of a few key traits. The interaction between traits and the environment may offer a resolution to this apparent paradox.

Diversification rates are likely to be dependent upon many interacting factors. To gain an overview of the general effects of the environment and its interaction with biotic traits, a broader sample across different lineages is required, yet at fine-enough scales to discriminate the environment in detail. A more detailed knowledge of angiosperm phylogenetic relationships at the level of genus or below would also provide the resolution and sample sizes needed to examine biological traits and particularly to evaluate complex models of trait and environment interaction. Ultimately, complete species-level analyses may be required to answer these questions.

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APPENDIX A. METHODS (ANGIOSPERM FAMILIES)

Eighty-six sister-family pairs were identified from the phylogenetic tree of Soltis *et al.* (1999, 2000). Sister-family comparisons are evolutionarily independent, and by relying on terminal clades difficulties of reconstructing ancestral values of study variables for much older nodes deep in the phylogenetic tree are avoided (Barraclough *et al.* 1998). Relative rates of molecular evolution were estimated by first pruning the phylogenetic tree to one representative taxon per family to remove possible bias due to the node density effect (Fitch & Beintema 1990) and then calculating maximum-likelihood branch lengths in PAUP* 4.0b10 (Swofford 2001) using the HKY85 model of DNA evolution with a gamma distribution to account for heterogeneity among sites. Because sister clades are the same age, branch length contrasts represent the relative rates of molecular evolution of the respective families.

Distribution maps for the sister families were obtained from Heywood (1993); distributions for families not included in this data source or those in which major taxonomic revisions had occurred were obtained from herbarium records at the Royal Botanic Gardens, Kew. Global datasets were collated for temperature (available from http://www.ngdc.noaa.gov/seg/eco/cdroms/gedii_a/datasets/a03/lc.htm), UV radiation (NASA/GSFC TOMS Team, available from <http://jwocky.gsfc.nasa.gov>), and

AET (available from <http://www.grid.unep.ch/data/grid/gnv183.php>), and a mean exposure per unit area was calculated for each family within ArcView (GIS 3.2, Environmental Systems Research Institute Inc.) together with total geographical extent, mean elevation (GTOPO-30, available from <http://edcdaac.usgs.gov/gtopo30/gtopo30.html>) and latitude (measured in degrees from the equator).

For each sister pair, A and B, the following contrasts were calculated: $\log(\text{number of species in A}) - \log(\text{number of species in B})$, and $X_A - X_B$, where X is either the mean coverage of the environmental variable or molecular branch length. To standardize the variance among contrasts, each contrast in species richness was divided by the age of the split between the sister families estimated from the gene sequence data as described in Wikström *et al.* (2001), area was cube-root transformed and the molecular branch length contrasts were divided by the mean of the branch lengths leading to both sister families (see Davies *et al.* (2004b) for further details).

The relationship between species richness, molecular rates and the environmental variables was explored by using least-squares regression through the origin in the statistical package R (R: a programming environment for data analysis and graphics, v. 1.60). To account for the possible effects of phylogenetic error, contrasts that had bootstrap support greater than 75% and were also represented in a recent comprehensive familial supertree of the angiosperms (Davies *et al.* 2004) were upweighted. Minimum adequate models were obtained for each analysis by removing parameters in a stepwise fashion, following Crawley (2002), and model criticism was performed to check for non-constancy of variance and non-normality of errors.

APPENDIX B. METHODS (IRIDACEAE)

Distribution maps for the terminal taxa represented in one of the two most parsimonious phylogenetic trees of Davies (2004), depicting relationships among 58 of the 65 currently recognized genera within Iridaceae, were compiled from herbarium records (Royal Botanic Gardens, Kew [K], Missouri Botanical Garden [MO] and New York Botanical Garden [NY]), published material (Innes 1985; Goldblatt & Henrich 1987), and field notes (P. Goldblatt and B. Mathew). Molecular branch lengths were calculated using the HKY85 model of DNA evolution, as described in Appendix A, from DNA-sequence data for six plastid regions (*rbcl*, *trnL* intron, *trnL-F* intergenic spacer, *rps4*, *rps16* intron and *matK*) split into two partitions: the first encompassing first and second codon positions (changes which may lead to amino acid substitutions), and the second partition encompassing third codon positions (mostly synonymous changes) and non-coding DNA regions.

Sister-taxon contrasts and least-squares regression was performed as described in Appendix A, with the exception that area was log transformed rather than cube-root transformed as this best met the assumptions of normality of errors in the subsequent analyses. A series of models were generated for subsets of sister clades represented in the phylogenetic tree, with and without weighting contrasts with nodal support values (see Davies (2004) for further

details). The model that was the most conservative with respect to the effect of phylogenetic error (weighted with bootstrap percentages and derived from non-nested contrasts) and missing taxa (collapsing clades in which missing taxa were thought likely to fall) was considered the preferred model.

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GLOSSARY

- AET: actual evapotranspiration
GIS: geographic information system