10 The Diversification of Flowering Plants through Time and Space: Key Innovations, Climate and Chance

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ABSTRACT

The flowering plants represent one of the largest terrestrial evolutionary radiations within recent geological times. Current estimates indicate there may be as many as half a million extant species, yet within the angiosperms species richness can vary over several orders of magnitude between closely related clades and between geographical regions. Understanding why some regions and some lineages contain more species than others has been a major challenge in biology. To date, approaches for studying these two patterns have been mostly separate. Traditional explanations for
taxonomic imbalance have focused upon key biological traits, whilst regional variation in species richness has been ascribed largely to environmental factors. Using a tree of life for flowering plants, we demonstrate that environment can explain much of the taxonomic imbalance evident within phylogenetic trees not explained by key traits, and unequal rates of diversification, a product of the interaction between traits and environment, may contribute to regional patterns in species richness.

10.1 INTRODUCTION

One of the principal goals of ecology and evolutionary biology is to understand the diversity and distribution of life on Earth. The expansion of molecular approaches to phylogenetics has provided a wealth of data for reconstructing the evolutionary events behind why some groups have flourished whilst others have floundered. Flowering plants (angiosperms) have been one focus for such studies. Flowering plants represent a highly species rich group with an estimated 500,000 extant species\(^1\)–\(^3\) and were the subject of early coordinated efforts to reconstruct a complete family level phylogenetic tree of a higher taxonomic group\(^4\),\(^5\). Flowering plant species richness varies greatly among taxonomic groups and geographic regions; traditionally such patterns have been treated as largely separate phenomena. Here we outline recent efforts to explore patterns and processes of diversification in flowering plants using large-scale phylogenetic trees.

The phylogenetic distribution of species richness can vary over several orders of magnitude, even between closely related families, indicating considerable variation in net diversification rates between clades. Fossil evidence suggests a first appearance of angiosperms in the Cretaceous\(^6\); however, early diverging lineages, such as Amborellaceae and Nymphaceae, tend to be relatively species poor. Furthermore, a number of more recently derived families are unexpectedly species rich, notably within Euasterids I\(^7\) sensu APG II\(^8\). There are two broad explanations for low species richness in older clades, either extinction rates have been higher, or speciation rates lower. Although the fossil record is insufficient to provide accurate estimates of extinction rates, there is little evidence that species poor clades were previously more diverse. It is therefore most likely that it was not until after the initial branching events of the clade that significant shifts in speciation rate arose\(^9\). Hence, high species richness is a result of elevated diversification rates within a subset of angiosperm lineages and therefore is of uneven distribution within flowering plants. However, the frequency, magnitude and location of shifts in diversification rates across the group have been poorly documented.

The geographical distribution of flowering plant species richness varies at a magnitude similar to that observed between lineages. Pollen records indicate ecological dominance was first attained at low latitudes between 20°N and 20°S\(^10\). Subsequent latitudinal expansion of the clade coincided with significant changes in the diversity of other plant groups, for example a decline in bryophytes and pteridophytes\(^10\). By the late Cretaceous flowering plants were the dominant flora of low latitudes, but comprised only 30–50% of diversity at higher latitudes. Over the past 65 million years before present (mybp) flowering plants have become the predominant vegetation type across all latitudes, but perhaps the most striking, and certainly the most frequently cited, spatial pattern in species richness remains the latitudinal gradient in diversity\(^11\). Tropical regions, for example Brazil’s Atlantic forest, the Eastern Arc and coastal forests of Tanzania/Kenya and Sundaland, are recognised hotspots of flowering plant species richness\(^12\). Species richness tends to decrease at higher latitudes, although there are a number of exceptions, notably within Mediterranean climates such as the Cape of South Africa, the Mediterranean basin and the Californian chaparral.

Numerous studies have sought explanation for why some lineages are more diverse than others, concentrating on the role of key biological traits, such as pollination syndrome, but in flowering plants (as in other groups) such traits apparently explain relatively little of the variation in species numbers. At the same time, ecological studies have explored the effects of environment on floristic richness within regions, but have not traditionally addressed evolutionary explanations as to why some lineages or regions have more species. Phylogenetics provides a means to combine these
approaches. Here we review how information on diversification rates inferred from phylogenetic trees can offer insights into the processes shaping both taxonomic and geographic patterns of species richness. Specifically, we consider whether differences in environment experienced by lineages can explain the extreme imbalance in species richness among clades.

10.2 MEASURING DIVERSIFICATION RATES

Among most organisms studied, it is commonly observed that relatively few taxonomic groups are species rich, the majority being species poor, and the shape of this frequency distribution has been termed the hollow curve (see Hilu, Chapter 11). Null models, such as the broken stick, typically fail to explain the extremes of the distribution. The lack of fit between empirical data and null expectations has been interpreted as revealing differences in speciation and extinction rates. However, contrasting species richness between higher taxa can be misleading and may be confounded by taxonomic artefacts. An alternative approach uses information from phylogenetic trees to infer diversification rates.

First, branching pattern of phylogenetic trees can provide information on the processes that shaped them. By comparing phylogenetic tree shape against an appropriate null model, it is possible to estimate whether diversification rates have varied significantly among lineages. Second, contrasts in species richness between sister clades provide a means to identify where large shifts in net diversification rates have occurred on the tree. Third, calibration of the branches on the tree allows estimation of absolute diversification rates. Conclusions drawn from such studies are, however, critically dependent upon the accuracy of the underlying estimate of phylogeny.

Until recently, insufficient phylogenetic information had been a limiting factor in our understanding and interpretation of the evolutionary history of flowering plants. The revolution in molecular techniques and phylogenetic methods in the 1990s saw an explosive growth in both the production and analysis of phylogenetic data, including the publication of a first draft of a phylogenetic tree for all flowering plant families. Molecular studies of more than 100 taxa are now commonplace. Davies et al. used a supertree approach to summarise this wealth of phylogenetic data in a single tree, providing the first complete representation of evolutionary relationships within flowering plants above the family level. Unlike traditional consensus methods, supertrees can deal with source trees that do not share the same terminal taxa. They are therefore able to provide a more comprehensive phylogenetic tree than any represented in the individual source trees on which they are based. Although supertree construction, particularly that based upon matrix representation with parsimony, has attracted some criticism, empirical results suggest it performs well.

Using the mean tree imbalance measure of Fusco and Cronk, as modified by Purvis et al., Davies et al. demonstrated that the uneven distribution of species richness among higher clades in the supertree of flowering plants was much greater than that predicted from a purely stochastic process, in which the propensity to diversify is equal across all lineages. It is possible that bias in supertree construction led to preferential resolution of imbalanced nodes; however, comparisons with nodal support metrics used in the source trees indicate that imbalanced nodes are as strongly supported as more balanced nodes. Furthermore, the supertree reflected the highly imbalanced topology of previous estimates of phylogeny based on incomplete sampling.

High tree imbalance suggests that speciation rates have been higher, or extinction rates lower, in some lineages over others. Sister cladecomparisons using the method of Slowinski and Guyer revealed numerous significant shifts in net diversification rates across all major clades (Table 10.1). Whilst there was some evidence for phylogenetic clustering of nodes subtending exceptionally imbalanced clades, for example, nodes falling within Lamiales, Asparagales and Caryophyllales, indicating a potentially heritable component to rate shifts, large shifts were evident throughout the tree topology.

The maximum likelihood estimate of diversification rate may be estimated as

$$\log_{N/t}$$
Reconstructing the Tree of Life

under the assumption that the diversification rate during time $t$ has been approximately exponential\cite{40,41}, where $N$ is the number of species in the clade, and $t$ is the time since the clade diverged from its sister clade on the dated tree. Shifts in net diversification rates were therefore calculated as:

$$\left(\frac{\log N_{(des)}}{t_{(des)}}\right) - \left(\frac{\log N_{(anc)}}{t_{(anc)}}\right)$$


\begin{table}
\centering
\caption{Taxonomic Distribution of Imbalanced Nodes Using the Imbalance Measure of Slowinski and Guyer\cite{20} on the Phylogenetic Tree of Flowering Plant Families from Davies et al.\cite{29}}
\begin{tabular}{llll}
\hline
Higher Clade & Order & Number of Nodes & % Imbalanced Nodes \\
\hline
N/A & Austrobaileyales & 2 & 50 \\
Magnolids & Canellales & 2 & 0 \\
Magnolids & Laurales & 6 & 33 \\
Magnolids & Magnoliaceae & 5 & 40 \\
Magnolids & Piperales & 2 & 50 \\
Monocots & Alismatales & 13 & 23 \\
Monocots & Asparagales & 20 & 30 \\
Monocots & Dioscoreales & 2 & 50 \\
Monocots & Liliales & 6 & 17 \\
Monocots & Pandanales & 4 & 0 \\
Commelinids & Commelinales & 4 & 25 \\
Commelinids & Poales & 14 & 36 \\
Commelinids & Zingiberales & 7 & 14 \\
Eudicots & Proteales & 1 & 100 \\
Eudicots & Ranunculales & 6 & 33 \\
Core Eudicots & Caryophyllales & 19 & 21 \\
Core Eudicots & Saxifragales & 11 & 36 \\
Asterids & Comales & 4 & 25 \\
Asterids & Ericales & 24 & 21 \\
Euasterids I & Gentianales & 5 & 20 \\
Euasterids I & Lamiales & 20 & 35 \\
Euasterids I & Solanales & 6 & 33 \\
Euasterids II & Apiaceae & 9 & 22 \\
Euasterids II & Aquifoliales & 4 & 25 \\
Euasterids II & Asterales & 11 & 27 \\
Euasterids II & Dipsacales & 1 & 0 \\
Rosids & Crossoxomatales & 2 & 0 \\
Rosids & Geraniales & 2 & 0 \\
Rosids & Myrtales & 10 & 10 \\
Eurosids I & Celastrales & 2 & 50 \\
Eurosids I & Cucurbitales & 6 & 17 \\
Eurosids I & Fabales & 3 & 100 \\
Eurosids I & Fagales & 6 & 17 \\
Eurosids I & Malpighiales & 27 & 22 \\
Eurosids I & Oxalidales & 4 & 0 \\
Eurosids I & Rosales & 7 & 29 \\
Eurosids II & Brassicales & 15 & 20 \\
Eurosids II & Malvales & 6 & 50 \\
Eurosids II & Sapindales & 9 & 22 \\
\hline
\end{tabular}
\end{table}
where des is the descendent clade and anc is the ancestral clade. A positive shift in net diversification rate indicates an increase in rates from the ancestral to the descendent clade. Mapping the magnitude of rate shifts on the topology of the tree confirms the impression of frequent large shifts in diversification rate, indicating that the propensity to diversify is a highly labile trait. However, the direction and magnitude of shifts in net rates appeared to vary nonrandomly across the phylogenetic tree.

The 10 greatest shifts in net diversification rates were negative, from high ancestral rates to low descendent rates, for example, the nodes subtending Ecteiocoleaceae (tussocky cord rush; one species) sister to Poaceae (grasses; c. 12,000 species), Stegnospermaceae (Cuban tangle; three species), sister to a number of families within Caryophyllales (for example, cacti, carpetweeds and fig-margitolds; c. 4,300 species), and Calyceaeae (calycera family; 40 species) sister to Asteraceae (daisies; c. 13,000 species). The two clades with the greatest positive shift in rates were identified as the sister family pair Moraceae (figs and mulberries; c. 1,675 species) and Urticaceae (nettles; 825 species). The mean age for the top 10 greatest positive shifts was significantly younger than that for the negative shifts (mean age 38.5 mybp versus 53.4 mybp for the positive and negative shifts respectively; \( P < 0.05 \), Mann-Whitney test).

In general, older nodes tended to exhibit greater taxonomic imbalance, associated with a negative shift in net diversification rates, and more recent nodes tended to be more balanced than expected, with several sister family pairs displaying correlated positive shifts in rates. One possible explanation for this would be a general increase in diversification rates within recent time periods, and the imbalance of older nodes might reflect the accumulated effect of past shifts in diversification rate. However, an alternative explanation is that this pattern reflects a bias due to the use of families as terminal taxa; shifts occurring within families can only be reconstructed as occurring in the entire family in the analyses. Furthermore, extinction will have had less time to operate within more recently derived clades, thereby inflating diversification rate estimates. The overriding impression is of a history littered with tales of evolutionary successes and failures. We explore what might explain this chequered past in the following sections.

### 10.3 KEY INNOVATIONS

Much emphasis continues to be placed upon the possession of a few key traits that might have influenced rates of diversification. By opening up new adaptive zones, such traits may have enabled those lineages that possess them to proliferate at an increased rate\(^{42}\). Salamin and Davies\(^{43}\) employed phylogenetically independent contrasts\(^{22}\) from the supertree of flowering plants to evaluate a number of putative key traits: generation time (herbaceous versus woody and annual versus perennial), dispersal (biotic versus abiotic), pollination (biotic versus abiotic) and sex (dioecy versus monoecy). Generation time might be negatively correlated to evolutionary rates\(^{44–46}\), resulting in greater evolutionary time over equivalent absolute time periods for fast-lived species. Biotic dispersal may enhance the probability of long-distance dispersal events\(^{44}\); further, both biotic pollination and biotic dispersal might reduce the frequency of outcrossing between geographically isolated populations, thereby providing the reproductive isolation necessary for allopatric speciation\(^{47,48}\). Among biotically pollinated taxa, monoecious species are more likely to have specialist pollinators\(^{49,50}\), further reinforcing reproductive isolation. Within monoecious taxa, selfing species may be more likely to form new species following hybridisation\(^{51}\), thereby enabling the establishment of isolated populations founded by rare dispersal events\(^{52}\).

The utility of phylogenetic trees in the comparative method in controlling for nonindependence and confounding variables is well recognised\(^{22,53}\). Independent contrasts provide a statistically powerful approach for identifying correlates of diversification. Any changes between sister taxa must have occurred since the time of divergence and thus represent independent evolutionary events. As sister taxa are the same age, comparisons of species richness directly reflect variation in net rates of diversification. Finally, the effects of confounding
variables, for example additional traits also affecting speciation rates, are minimised\(^4\). However, Salamin and Davies\(^3\) found no significant association between the traits studied and species richness among higher clades.

There are several possible explanations as to why no support was found for the key innovation hypothesis:

- **Poor phylogenetic data**: phylogenetic error will tend to reduce signal and thereby increase the probability of type II errors when independent contrasts are employed\(^2\).
- **Poor trait data**: if clades were miscoded in terms of trait value, we would also predict an associated increase in type II error rates.
- **The wrong traits were examined**: Gorelick\(^5\) lists 20 hypotheses that have variously been proposed to explain the evolutionary success of the flowering plants, including many key traits. Doubtlessly a comprehensive survey of the literature would reveal many more putative key innovations, and a number of significant results have been reported within a subset of clades\(^3,56-60\). It is possible that, if sufficient data were to become available to test these hypotheses in the future, significant associations may be found across the flowering plants.
- **Contingency upon other traits and the environment**: whether a certain trait influences diversification rates is likely to depend on a number of factors, including the abiotic environment, other biological traits, and other taxa\(^6\).
- **Contrasts at higher taxonomic levels may be too insensitive**: the majority of flowering plant diversity is encompassed within, rather than between, families, hence a stronger association between traits and species richness might be observed for more fine-scale analyses.

Although there were a possible 378 contrasts (nodes in the supertree), the sample size of unambiguous state changes was small; life form and mode of pollination were both limited to two comparisons, the maximum being 15 comparisons (mode of dispersal). The limited number of contrasts was partly a product of lack of variation in the traits under examination; for example, abiotic pollination characterises both clades subtending the most imbalanced node identified above, the grasses and their sister group. However, the predominant limiting factor was within family variation, resulting in many clades being classified as polymorphic for the majority of traits, indicating that, for the traits examined, the taxonomic scale of this analysis was inappropriate.

Where strong associations between species richness and biological traits have been found, they are often environment or clade specific, for example, annual life form in grasses\(^3\), floral nectar spur characterisation in columbines\(^5\), climbing habit in predominantly tropical taxa\(^6\) and fleshy fruit in the tropical understorey\(^9\). As we look further back in time, at nodes deeper in the phylogenetic tree, we would expect a proportional increase in the impact of other factors, such as mass extinctions, biogeography and other traits on diversification rates\(^61,62\). The difference between the findings of Smith\(^9\) and those of Salamin and Davies\(^3\) on the importance of biotic dispersal, for which fleshy fruit is an indicator, is likely a result of the former study restricting comparisons to taxa found only within a narrow environmental niche, the tropical understorey. The significant association between annual life form and species richness in grasses and the absence of significance in contrasts between families of flowering plants is also a likely product of scale, but taxonomic rather than environmental. It is therefore unsurprising that key traits do not always generalise across disparate taxa. For example, biogeography appears to have left a greater imprint on patterns of current species richness than presence or absence of nectar spur in the genus *Halenia*\(^6\), yet nectar spurs may remain important when only young, geographically restricted, clades are considered.

In summary, there is a growing appreciation that explanations based upon one or a few traits are too simplistic to explain patterns of flowering plant species richness\(^7,8,64\). Where significant correlations between biological traits and species richness have been found, they tend to be in comparisons between recently radiated taxa sharing similar ecological conditions. Whether a biological trait influences net diversification rates is therefore likely to depend on a number of other
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factors, including abiotic environment. If the efficacy of a trait in influencing speciation rates were environment dependent we might also predict that different traits would have been advantageous at different geological times, with those taxa that happened to be pre-adapted to changes in environmental conditions radiating rapidly. Such a scenario has been suggested as explaining the rapid radiation of the grasses (previously restricted to marginal habitats) coinciding with the late Tertiary change towards a drier climate, which enabled the exploitation of new niches and a dramatic increase in their ecological dominance\(^{65,66}\), and might explain the apparent lag between the origin of particular traits and the increase in the proportion of taxa possessing them in the fossil record\(^{67}\).

Environment clearly has the potential to greatly enhance our understanding of the evolutionary history of flowering plant diversity; in the following section we explore the effects of one aspect of environment, namely latitudinal gradients.

### 10.4 EVOLUTIONARY RATES AND THE LATITUDINAL GRADIENT IN SPECIES RICHNESS

One of the most pervasive patterns in ecology is the latitudinal gradient in species richness. In most taxa, species richness tends to be greatest at the equator and declines towards the poles\(^ {68}\). Despite the wealth of literature on this phenomenon, the underlying causes remain unclear\(^ {69,70}\). One possible explanation is that high levels of environmental energy promote higher species richness nearer the equator\(^ {71–73}\). This hypothesis is supported by observations that energy-rich regions tend to support more species than energy-poor regions\(^{74–78}\). Energy gradients can explain c.70–80% of the variation in species richness between regions\(^ {79}\). The existence of alternative gradients in species richness, for example those with altitude and depth, provide additional support for a species–energy relationship\(^ {72}\). Furthermore, when energy is controlled for, the latitudinal gradient in species richness can disappear\(^ {79}\), suggesting that in many cases the latitudinal gradient in species richness may be more accurately described as an energy gradient. The reasons why species richness might vary with energy are examined below.

#### 10.4.1 BIOMASS THEORY

Higher productivity at lower latitudes might allow a greater biomass and hence more species to be supported\(^ {80,81}\). Wright\(^ {71}\) formally stated the species–energy theory as an extension of the species–area theory. Wright argued that area was a surrogate measure of available resources; a direct indicator of resource availability, such as energy, would therefore provide a more accurate predictor of species richness. This assumes that energy-rich environments support more populations rather than simply more individuals per population. The lack of a consistent relationship between productivity and species richness has led some to largely dismiss this theory\(^ {69}\), but a better understanding of the effects of spatial scale and resource partitioning upon these relationships may provide a clearer picture\(^ {82,83}\).

#### 10.4.2 FASTER EVOLUTION HYPOTHESIS

Increased environmental energy speeds up evolutionary rates and species production. Rohde\(^ {72}\) argued that the higher diversity of the tropics could be explained by greater effective evolutionary time. The higher temperature of tropical regions may increase metabolic rates and decrease development times, leading to shorter generation times, faster mutation rates, and as a consequence, a faster response to selection pressures (Figure 10.1a). The faster evolution hypothesis assumes that environment-mediated variation in diversification rates is sufficient to produce geographical gradients in species richness. If correct, we would expect variation in diversification rates between clades encompassing areas with different energy loads. The faster-evolution hypothesis is consistent with the tropics as a cradle of diversity\(^ {84–87}\). Previous work established a link between evolutionary rates, estimated from sequence divergence data, and species richness in flowering plants\(^ {88,89}\), one step in the faster evolution theory. However, a study of evolutionary rates in birds by Bromham and
Cardillo failed to find any association between molecular rates and latitude; the second step in the theory. Therefore, despite widespread interest, support for the faster evolution hypothesis has been equivocal, and the direction of causality unclear (compare Figure 10.1a and Figure 10.1b).

### 10.4.3 Evaluating the Faster Evolution Hypothesis

Davies et al. reviewed evidence for the faster evolution hypothesis using estimates of energy load across families of flowering plants derived from GIS data, based upon contemporary distributions. As different aspects of the environment might influence evolutionary rates versus biomass more strongly in plant taxa, three energy measures were employed: ultraviolet (UV) radiation, actual evapotranspiration (AET) and temperature. UV radiation might influence mutation rates via the formation of harmful photoproducts and has been described as a driving force in evolutionary rates. AET represents water-energy dynamics and reflects the amount of biomass an area can support; it is often strongly correlated with regional plant species richness. Finally, temperature might have an effect on both biomass and rates of molecular evolution. Therefore, if the faster evolution hypothesis were correct, we would predict that UV or temperature would display the stronger relationship with species richness, via an intermediate link with molecular evolutionary rates.

Present day distributions and climate might provide a poor estimate of conditions experienced over evolutionary time. Families of flowering plants range in age from c. 25 mybp (for example, Moraceae, Urticaceae and Asteropeiaceae) to >100 mybp (for example, Amborellaceae, Nymphaeaceae and Chloranthaceae), while climatic shifts occur in the order of every 10,000–100,000 years. It may therefore seem unrealistic to expect contemporary measures to provide a useful index of past environment. However, correlated range dynamics amongst related but disjunct taxa indicate ecological niche conservatism over time periods spanning tens of millions of years. Environmental tracking by plant lineages can result in a migration like response to climatic change; hence mean environment for a plant lineage might be relatively constant over time. Although geographical barriers are likely to prohibit exact environmental matching, if contemporary environment was independent from the environmental conditions experienced over evolutionary time, it would most likely confound attempts to detect true relationships, particularly those with evolutionary variables such as rate of molecular change.
Sister family comparisons of Davies et al.\textsuperscript{91} supported the broad predictions of the species–energy theory, revealing a strong correlation between environmental energy and species richness. Temperature was the best predictor of the alternate energy measures, explaining 19\% of the variation in species numbers between families, once area had been accounted for. Energy was also found to be a good predictor of molecular evolutionary rates, with faster rates in high-energy environments, confirming the second step in the faster evolution theory. Although a relationship between molecular evolutionary rates and environmental energy had not previously been reported\textsuperscript{90}, there was no evidence that energy increased diversification rates by this pathway. Instead the effects of energy on both molecular rates and species richness was direct (Figure 10.1b), leading Davies et al.\textsuperscript{91} to reject the faster evolution hypothesis.

Diversification rates co-vary with environment; lineages occupying higher energy regions tend to have higher net speciation rates. The direct link between energy and species richness is compatible with the biomass hypothesis. More productive environments might reduce extinction through supporting higher population densities, thereby elevating net diversification rates, although the precise relationship between productivity and density remains controversial\textsuperscript{70,98–100}. Bonn et al.\textsuperscript{101} recently proposed an alternative explanation, in which more productive environments were likely to contain a greater sample of taxon-specific critical resources. Therefore, high energy environments could sustain a greater number of viable populations, not by increasing population density, but rather increasing the probability of the occurrence of a limiting resource, which may vary between taxa. This hypothesis remains to be evaluated in plants.

Both environment and biological traits may explain a proportion of the variation in net diversification rates among lineages within flowering plants. Key traits are difficult to evaluate for older nodes; similarly, we might expect causal relationships between environment and species richness to be more difficult to detect for more ancient splits due to post speciation range movement and historical climate change. In the final section of this chapter, we explore how combining information on biology and environment can be mutually informative, using the iris family (Iridaceae) as a test case. By using younger and more narrowly distributed taxa, it may be possible to more accurately discriminate environment and the effect of species-specific traits on geographical and taxonomic patterns of species richness.

### 10.5 TRAITS × ENVIRONMENT: DIVERSIFICATION OF IRISES IN THE CAPE OF SOUTH AFRICA

We contend that species richness of a clade depends on both biological traits and the environment. In similar environments biological traits might therefore be predicted to explain much of the variation in species richness between taxa. For taxa sharing similar traits but occupying different habitats, environment will be the major determinant of species richness. However, it may more often be the case that the interaction between traits and environment will predominate. The interaction term might be positive, neutral or negative\textsuperscript{61}.

The Cape Region of South Africa is renowned for its high levels of plant species richness and endemism but is an outlier from global trends relating environment to flowering plant species richness\textsuperscript{102–106}. However, it is possible that clades containing lineages that have radiated extensively in the Cape, such as the iris family, are characterised by biological traits that have resulted in a different functional response to the environment that can still explain geographical variation in species richness. If the influence of the biological traits on diversification rates within these clades were environment dependent, we would first predict that Cape clades lacking those traits would be species poor and, second, that non-Cape clades would be species poor regardless of the traits that define them.

Irices are a highly diverse family of perennial herbs with around 1,800 species in 65 genera\textsuperscript{107}, including several familiar cultivars of well known genera, for example \textit{Crocus}, \textit{Gladiolus} and \textit{Iris}. Adapted to neither the intense competition for light nor the rapid growth required for gap colonisation...
within dense vegetation typical of tropical regions, species numbers tend to be highest in seasonally
dry environments (Figure 10.2). Irises conform to typical patterns of Cape diversity: the family
contains 677 species in the region, of which 80% are endemic \(^{105}\), and many genera including
Gladiolus (260 species) and the peacock irises (Moraea) (196 species) have radiated extensively
within the Cape \(^{108}\). Although a few genera such as Neomarica (eight species) and Eleutherine (two
species) are found in the Neotropics, they are relatively species poor. The family is characterised
by an isobilateral leaf held vertically, perhaps the single most important morphological innovation
of the family, and underground storage organs, such as a corms (for example, Crocus and Gladiolus),
rhizomes (for example, Isophysis and Sisyrinchium) or bulbs (for example, Cypella and Tigridia).
Floral morphology is highly variable and matches several different pollination syndromes \(^{109}\). These
traits have been thought important in the group’s evolution within the Cape \(^{105}\).

Phylogenetically independent contrasts \(^{22}\) of species richness from a generic level phylogenetic
tree of irises revealed several significantly imbalanced nodes \(^{110,111}\). Although the node subtending
Isophysis (one species) and the remainder of Iridaceae is the most imbalanced, the next most basal
nodes are also highly imbalanced, suggesting that that the ancestral state may have been a low net
diversification rate. The early diverging lineages, Diplarrhena (two species), Patersonia (21 species)
and Geosiris (one species), tend to be species poor, rhizomatous, of limited geographical distribution
and suggest an Australasian origin for the family. Repeating the family-level analysis of environment
and species richness at the generic level showed that abiotic environment plus area could explain
up to 85% of the variation in species richness between sister clades, including the highly imbalanced
nodes identified above.

Environmental factors associated with warm, dry and topologically diverse habitats were the
best predictors of species richness, reflecting the specific preferences of the family and confirming
its departure from the more general trend towards higher species richness in tropical environments.
However, environment alone was insufficient to explain the high diversity of Cape clades. By using
contrasts between sister clades, lineages within the Cape were revealed to have speciated at faster
rates than those found elsewhere, even than in regions with similar Mediterranean type climates.
Molecular evidence suggests that the Cape may have undergone a period of rapid diversification
coinciding with a change in oceanic currents leading to the aridification of the region 8–7 mybp \(^{104,112}\).
While the majority of branching events in the generic phylogenetic tree predate this shift in climate,
there is evidence in at least one genus, *Moraea*, that this geological background provided the setting for the diversification leading to high species richness of irises in the Cape. It is possible that the high net diversification rates observed in Cape clades are a product of abiotic factors not included in the model parameters or that the spatial scale of the analysis was too insensitive to accurately characterise the great physical diversity of the Cape Region. For example, the Cape may have been more climatically stable during the Pleistocene radiations, allowing greater time for gradual speciation, elevating net diversification rates. However, of the genera with the greatest deviation from the model, all those that contain more species than predicted by environment, *Geissorhiza*, *Hesperantha*, *Ixia* and *Therianthus*, fall within a single clade, Crocoideae. Although no biological traits changed state frequently enough on the tree to allow tests for a general correlation with diversity, a number of traits are characteristic of this clade and may have been instrumental in its diversification in the Cape. The evolution of the perianth tube and zygomorphic flowers was likely important in allowing floral plasticity in Crocoideae, and subsequent pollinator specialisation. A cormous rootstock, again typical of Crocoideae, may have enabled rapid regrowth in fire-dominated landscapes and also promoted establishment by vegetative reproduction following rare long-distance dispersal events.

Even if sufficient data were available to evaluate these putative key traits more rigorously, it seems unlikely that they would be identified as key innovations from simple analyses of taxonomic imbalance, as several species poor genera share many of these traits with their species rich counterparts. Ancestral state reconstructions for both flower symmetry and rootstock type reveal that shifts in character states are correlated with neither significantly imbalanced nodes nor large deviance from the expected values derived from the climate variables. Biological traits associated with high species richness in genera of irises may therefore have only had those effects in particular places, most notably the highly heterogeneous environment of the Cape. This is consistent with our second prediction: clades outside the Cape have not diversified, irrespective of their intrinsic biological attributes. The limited number of comparisons meant that it was not possible to examine our first prediction: whether the absence of particular traits results in lower diversification rates in the region.

**10.6 CONCLUSIONS**

Phylogenetic trees of the flowering plants are too imbalanced to be a product of an equal rates Markov process, in which all lineages have an equal probability of diversifying, 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. If the influence of heritable biological traits upon the likelihood of diversifying was dependent on environmental conditions and environmental change was frequent, repeated shifts in diversification rate would be expected. Within any set of conditions some lineages would be favoured over others. However, the identity of these lineages would fluctuate with a changing environment, as conditions favourable to speciation within one lineage may not be so in another. A strong relationship between environment and species richness would, however, be evident at any single point in the evolutionary history of flowering plants.

Extant species richness may be best explained with reference to the contemporary environment. However, lineages characterised by different suites of traits might be expected to display different functional responses to their physical surroundings. Irises represent a family that departs from global trends in species richness, yet the environment can explain a large proportion of the variation in species richness among lineages. Even within this clade, it is likely that particular biological traits have favoured rapid diversification within the Cape of South Africa. A wider sample of Cape clades may provide sufficient data to evaluate the interaction between traits and environment in this unique and species rich region.
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