Plant species radiations: where, when, why?

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The spatial and temporal patterns of plant species radiations are largely unknown. I used a nonlinear regression to estimate speciation and extinction rates from all relevant dated clades. Both are surprisingly high. A high species richness can be the result of either little extinction, thus preserving the diversity that dates from older radiations (a 'mature radiation'), or a 'recent and rapid radiation'. The analysis of radiations from different regions (Andes, New Zealand, Australia, southwest Africa, tropics and Eurasia) revealed that the diversity of Australia may be largely the result of mature radiations. This is in sharp contrast to New Zealand, where the flora appears to be largely the result of recent and rapid radiations. Mature radiations are characteristic of regions that have been climatically and geologically stable throughout the Neogene, whereas recent and rapid radiations are more typical of younger (Pliocene) environments. The hyperdiverse Cape and Neotropical floras are the result of the combinations of mature as well as recent and rapid radiations. Both the areas contain stable environments (the Amazon basin and the Cape Fold Mountains) as well as dynamic landscapes (the Andes and the South African west coast). The evolution of diversity can only be understood in the context of the local environment.

Keywords: diversification; species richness; extinction rate; speciation rate; environmental stability; dynamic environments

1. INTRODUCTION

A radiation is the increase in diversity in a lineage; consequently, all biological diversity is the result of radiations. Several types of radiations have been proposed. Adaptive radiations (Baldwin 1997; Givnish & Systma 1997; Sanderson 1998) relate an increase in diversity to a particular adaptation to some environmental features, or as diversification into a new habitat. Ancient radiations refer to events that occurred mostly before the Neogene, and which generated divergent phylogenetic lineages (e.g. families or tribes), but not necessarily species richness (Whitfield & Lockhart 2007). The third type of frequently invoked radiations is 'recent and rapid radiations'. Although these have recently received some attention (Richardson *et al.* 2001*a*,*b*; Klak *et al.* 2004; Hughes & Eastwood 2006), there is no adequate definition of how 'recent' and how 'rapid' a radiation has to be to fit this definition, nor is an adequate terminology available to describe radiations that are not recent and rapid.

Plant diversity is not globally evenly distributed (Mutke & Barthlott 2005). There has been substantial research into the ecological correlates of species diversity (e.g. Rosenzweig 1995; Francis & Currie 2003; Hawkins *et al.* 2003), and the more impressive models can explain substantial variation in species diversity. Recently, there has also been an increased appreciation of the importance of the historical processes that generate diversity in explaining the patterns of modern diversity (Ricklefs 2004, 2006*a*; Stevens 2006; Kreft & Jetz 2007). The conditions under which rapid diversification happens have hardly been explored, although the importance of new habitats (Setoguchi *et al.* 1998; Hughes & Eastwood 2006), climatic stability (Cowling & Lombard 2002) and a fragmented landscape (Qian & Ricklefs 2000) has been highlighted.

Here, I use all relevant dated radiations to explore under what circumstances radiations occur. I show that it is possible to make a distinction between recent, rapid radiations and older, mature radiations. Both can result in substantial species diversity. Recent and rapid radiations are associated with new habitats, mostly the result of geotectonic changes. Mature radiations, by contrast, are found in areas of tectonic and climatic stability, and could be the result of persistence where there has been no major extinction. Thus, different historical processes can lead to similar patterns of modern species richness.

2. MATERIAL AND METHODS

(a) *Assembly of the data, criteria for selection and potential biases*

I assembled a dataset comprising clades that met three conditions. First, the crown groups should be defined and monophyletic, allowing a reasonable estimate of the number of included species. In most cases, positive evidence for the monophyly of the groups was available, except for one case where monophyly, though likely, was neither supported nor contradicted by the molecular phylogenetic data. Second, the crown group should be dated. It is generally better to use stem ages, as this includes the extinctions preceding the crown radiation (Ricklefs 2007). However, dated crown groups are more commonly available than dated stem groups. In all

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One contribution of 12 to a Theme Issue 'Speciation in plants and animals: pattern and process'.

instances these were molecular, rather than fossil, dates. The precision and reliability of these dates is dependent on a number of issues: the rate-correcting methods used (Renner 2005; Rutschmann 2005); the sampling (Linder *et al.* 2005); and the calibrations used (Magallón 2004). Several methods were used for the study groups, and although it would have been desirable, it was beyond the scope of this investigation to recalculate all the datings using the same methods. Lastly, the clades had to be more or less geographically restricted. In many cases, a small minority of the species is also found outside the focal areas; these were included in the diversity counts. In total, 70 clades were identified (electronic supplementary material), of which 68 can be more or less grouped to the following focal areas: the Andes (11 clades); the Greater Cape Floristic Region (18 clades; Born *et al.* 2006); Australia (14 clades); New Zealand (8 clades); the tropical regions of Africa and South America (7 clades); and Eurasia (10 clades).

Especially among the older clades, there could be a bias in the data towards more species-rich clades, since many of them were dated in search of recent and rapid radiations. Small or 'normal' clades are not likely to receive much attention. Curiously, a number of the really interesting large clades have not yet been dated. These include the genus *Erica* from Southern Africa (approx. 800 species), the phyllodinous *Acacia* clade from Australia (approx. 900 species) and *Carex* from the North temperate regions (approx. 1700 species). There are also some potentially very interesting areas from which not enough clades have been investigated, these include Southeast Asia, the eastern Himalaya and the Brazilian Atlantic forests.

(b) Calculation of radiation and extinction rates

The current species richness of a clade is a function of the age of the clade and the net diversification rate (r). The net diversification rate is the difference between the speciation rate (λ) and the extinction rate (μ). If we assume no extinction, then the number of species (N) in a clade is (Kendall 1948)

$$N(t) = e^{\lambda t}, \tag{2.1}$$

where N is the diversity and t is the time in millions of years. If we include the extinction rate in equation (2.1) and assume that the rates are constant over time (Ricklefs 2007), then we can calculate the predicted number of species in a clade to be (Harvey *et al.* 1994; Magallón & Sanderson 2001; Ricklefs 2006b)

$$N(t) = \frac{\lambda e^{(\lambda - \mu)t} - \mu}{\lambda - \mu}. \tag{2.2}$$

This is dependent on the survival of the clade—with neontological data, extinct clades become invisible. Instead of the extinction rate μ, Ricklefs (2006b) suggested using the ratio κ of extinction to speciation, and this results in the following equation for stem groups:

$$\ln(N) = \ln(\exp[\lambda(1 - \kappa)t] - \kappa) - \ln(1 - \kappa). \tag{2.3}$$

Since I used crown groups, equation (2.3) needs to be corrected to

$$\ln\left(\frac{N}{2}\right) = \ln(\exp[\lambda(1 - \kappa)t] - \kappa) - \ln(1 - \kappa), \tag{2.4}$$

as crown groups at their first recognition contain two species. The values for λ and κ were estimated by a nonlinear regression, minimizing the sum of the squared residuals, and

using sequential quadratic programming as implemented in the software package SPSS, against the observed data.

In order to obtain the speciation rate for the individual clades, the proportional extinction rate κ was fixed at various levels (0.999, 0.95, 0.9 and 0.85, chosen based on the results of the nonlinear regression). The different κ levels were used to bracket the possible extinction rates. Using (Ricklefs 2006b)

$$\lambda = \ln[N(1 - \kappa) + \kappa]/(1 - \kappa)t, \tag{2.5}$$

we can calculate the speciation rate λ for each clade for each fixed level of κ. Equation (2.5) can be corrected for crown groups by dividing the number of extant species by half, resulting in

$$\lambda = \ln[(N/2)(1 - \kappa) + \kappa]/(1 - \kappa)t. \tag{2.6}$$

Note that all these equations assume that the speciation and extinction rates do not change through time.

(c) Correlates of radiations

The speciation rate λ (calculated using equation (2.6)) was used as a measure of the radiation rate for each clade. The effects of variation in the extinction rate were investigated by fixing four different levels of the proportional extinction rate κ. Four potential correlates of variation in the speciation rate were investigated: the ages of the crown groups; the geographical region; the environmental stability; and the geographical area available.

The ages of crown groups ('CladeAge') were used to evaluate whether the diversification rate changes over time. As the available phylogenies were not fully sampled and dated, only a single speciation rate (and consequently diversification rate) could be calculated for each clade. For young clades, this measures the diversification rate during the early stages of the existence of the clade. However, for older clades, it contains an average of the diversification rate during the early combined with the later stages of the clade's existence. It is not possible to obtain an estimate of the diversification rate of only the later stages, as we have neither branch length data, nor internal calibration points. The geographical regions ('region'; table 1) were evaluated to determine whether there are any simple regional effects. The environmental stability ('stability') is a crude characterization of the time since dramatic environmental changes. These were simplified into three categories: recent (Late Miocene or later, i.e. New Zealand and the Andean páramo); intermediate (Miocene, i.e. Europe); and old (stabilized by the Oligocene, i.e. Australia and the Cape). The geographical areas ('area') are approximate. In order to obtain a more-or-less normal distribution of the values, all continuous parameters were ln transformed, except for the geographical area, which was log transformed.

Generalized linear models (GLMs), implemented in the statistics software package SPSS, were used to investigate the relationship between ln(speciation rate λ) and ln(CladeAges) in combination with the three other factors (regions, stability and area). Since the regions are subdivisions of the three stability classes, these two parameters could not be analysed in combination.

3. RESULTS

(a) Global radiation rate

The proportional extinction rate κ and speciation rate λ were estimated by nonlinear regression to be $\kappa = 1 \pm 0.008$, CI $= 0.984 - 1.016$ and $\lambda = 2.842 \pm 0.730$,

Table 1. Regions and their attributes.

region	area (×1000 km²)	stability	definition (biomes)
Andes, South America	1700	recent	alpine areas and slopes of the Andes (alpine and montane forest biomes)
Cape, southwestern Africa	90	old	Greater Cape Floristic Region (heathland, semi-desert biomes and temperate forest)
New Zealand	270	recent	whole archipelago (alpine, montane forest, semi-arid and temperate forest)
Australia	7682	old	whole continent (heathland, temperate forest, alpine, savannah and rainforest biomes)
tropical	10 000	old	tropical America and Africa, both dry and wet (rainforest, savannah and semi-arid biomes)
Eurasia	15 000	intermediate	temperate zone, including the Mediterranean basin (alpine, temperate forest, heathland, steppe, boreal and arctic biomes)

CI = 1.383–4.300. These should be interpreted as events per million years. The regression explains 12.2% of the variance in the data (figure 1).

Fixing the proportional extinction rate κ at lower levels results in a dramatic decrease in the predicted speciation rate λ (figure 2), but then the older lineages in our sample are overpredicted (figure 1). To test whether the very high extinction rate is needed to account for the older lineages, we reanalysed the data including only clades younger than 30, 10 and 5 Ma, but this does not change the extinction rate and the surprisingly high value of κ is found by all analyses.

(b) *Correlates of diversification*
The effect of clade age investigated with a linear regression gives a weakly significant negative result ($r^2 = 7.2\%$, d.f. = 1,65, $F = 6.152$, $p = 0.016$). The geographical area of the separate regions showed no significant relationship to λ. Two sets of significant results were obtained: the model relating $\ln(\lambda)$ to $\ln(\text{CladeAge})$ plus the regions ($r^2 = 16.4\%$, d.f. = 6, $F = 3.167$, $p = 0.009$; $\ln(\text{CladeAge})$: d.f. = 1, $F = 14.854$, $p = 0$; regions: d.f. = 5, $F = 2.434$, $p = 0.045$); and relating $\ln(\lambda)$ to $\ln(\text{CladeAge})$ plus stability ($r^2 = 16.3\%$, d.f. = 3, $F = 5.291$, $p = 0.003$; $\ln(\text{CladeAge})$: d.f. = 1, $F = 13.877$, $p = 0$; stability: d.f. = 2, $F = 4.527$, $p = 0.015$).

Fixing a lower extinction rate κ (e.g. at 0.95, 0.9 and 0.85), and calculating the speciation rate λ for each clade, massively accentuates the differences over time, so that the speciation rates are estimated to be much higher for younger clades than for older clades. As a result, the variance explained by the GLMs is much increased, and, at $\kappa = 0.85$, the $r^2 = 55\%$ and coefficients of the regions are significant at 0.03 and coefficients of stability are significant at 0.009.

4. DISCUSSION
(a) *Classification of radiations*
Both the speciation rate λ of 2.842 ± 0.730 and the proportional extinction rate κ of almost 1 ± 0.008 are remarkably high, implying rapid speciation followed quickly by the loss of almost all products from that speciation. Magallón & Sanderson (2001) suggested that the proportion of species that become extinct (their ε is the same as κ of Ricklefs) should be less than
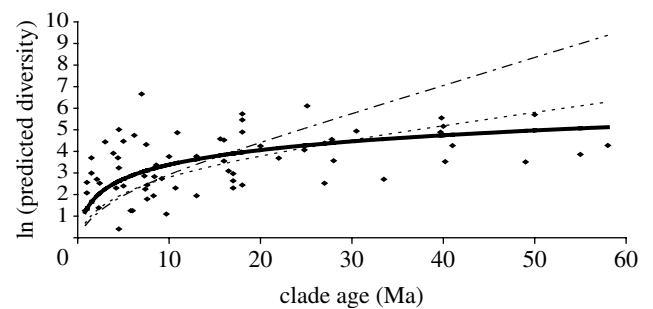

Figure 1. Relationship between clade age and species richness. The filled diamonds indicate observed diversity. The solid line is the predicted diversity from the nonlinear regression (equation (2.4)), with $\lambda = 2.848$ and $\kappa = 1$. The dotted line is with κ fixed at 0.95 and the dot-dashed line with κ fixed at 0.85.
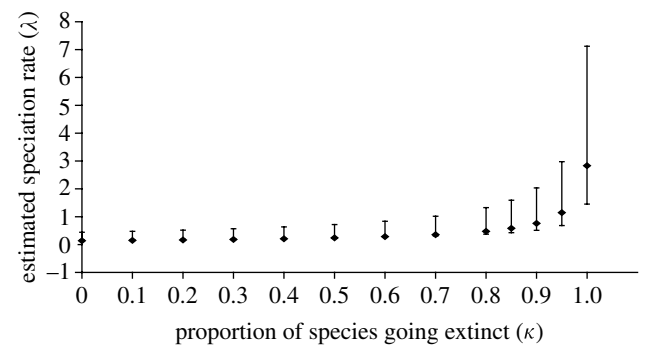

Figure 2. Predicted speciation rates for the current dataset at various proportional extinction rates. The upper and lower intervals are the 95% CIs.

0.9, based on the argument that the speciation and extinction rates over one event per million years (which are implied by higher extinction rates) had not been observed in the fossil record, and that high rates could become chaotic. However, the estimates from the fossil record are based on a restricted number of animal clades; it is possible that plant species could show greater turnover rates. Furthermore, Ricklefs (2006b) obtained similarly high extinction rates in an analysis of American passerines ($\kappa = 0.938 \pm 0.076$). Forcing the proportional extinction rate down results in more normal speciation rates. However, our data, using only crown groups, probably underestimate the extinction rate and, as such, underestimate speciation rates.

These results suggest that extinction rates, and consequently speciation rates, might be higher than previously expected.

However, the assumption that the speciation and extinction rates do not change over tens of millions of years may be a gross oversimplification. If they do change, then a single speciation and extinction rate is fairly meaningless. The apparent accuracy of the proportional extinction rate could be a side effect of the impossibility of the extinction rate being 1. As the estimated rate approaches this boundary value, the estimation of the error becomes more difficult.

Younger clades show a higher diversification rate than older clades, suggesting that the diversification rate for each clade changes from initially rapid to slower later. This is supported by the significant negative relationship between clade age and speciation rate, as a proxy for the diversification rate, especially if the effect of the geographical regions and their intrinsic ages is removed. The data here underestimate the differences in the rates in the early and later phases of the clade's history, since we do not have an undiluted estimate of the later diversification rate. We can use this change in the diversification rate to recognize two phases in the radiation of a clade. During the first phase of a radiation, the rate of increase in the diversity is very rapid. This phase lasts during the first 2–8 Ma. Fitting the regression to clades that are up to 10 or 5 Ma old results in a higher estimate of λ (3.78 ± 2.52 and 6.658 ± 5.4) while κ remains the same (1 ± 0.057 and 1 ± 0.069). This is the typical phase of recent and rapid diversification, as has been illustrated for the South African Aizoaceae (Klak *et al.* 2004) and the South American *Lupinus* (Hughes & Eastwood 2006). However, the large errors around these estimates, resulting from the small number of clades available in these age categories, warn against paying too much attention to these numbers.

During the second phase of the radiations, the diversity in the clades increases only slowly. The current high diversity in these clades is at least in part due to past high diversification, and we would expect a lineage through a time plot to show a gradual decrease, as has been documented for Restionaceae (Linder *et al.* 2005). This sort of radiation can be referred to as 'mature'. High diversity resulting from mature radiations is more a result of the absence of episodic mass extinctions, rather than a particularly high speciation rate. This appears to be a common pattern in the Cape and Australian floras (Crisp *et al.* 2004).

The change in the diversification rate documented here is comparable to the recuperation in diversity after mass extinctions, when an initial rapid increase in diversity (a recent and rapid radiation) is followed by a stasis or plateau in species richness (equivalent to a mature radiation; Stanley 1979). This pattern could result from three factors. First, the speciation rate could slow down in older clades. Such a slowdown in the speciation rate is often predicted on the argument that the available niches have become filled, and that there is some sort of equilibrium diversity (Benton & Emerson 2007). Second, the extinction rate in older clades could increase. Such an increase could also be predicted, as the niches become more finely divided

with increasing species richness, thus potentially reducing the niche width of each species and so making them more susceptible to extinction resulting from climatic fluctuations (Dynesius & Jansson 2000; Jansson & Dynesius 2002). Finally, both factors could operate. We cannot at this stage distinguish between these possible explanations. If a larger dataset were available, it may be possible to model the speciation and extinction rates.

(b) *Effect of area*

The absence of a relationship between the area of the regions on the net diversification rate is unexpected, as it has been suggested that large areas should encourage speciation rates and retard extinction rates (Rosenzweig 1995; Chown & Gaston 2000). However, area is a surprisingly complex issue. If area is interpreted as the available habitat rather than the geographical area, then it can change dramatically through evolutionary time (Fine & Ree 2006). The same global climatic change (e.g. Holocene warming) could result, for any given habitat, in an areal restriction in one region and an expansion in another (e.g. Ehrich *et al.* 2007). Most discussion deals with the area available to each species, and not necessarily with the area available to whole clades. The lack of a relationship between area and diversification rate in this analysis could be because the clades used often do not neatly group into regions. Furthermore, the habitat diversity in the regions ranges from fairly narrow (e.g. the Cape) to very wide, and including several biomes (e.g. Australia, North temperate). Comparing the areas of these regions might be meaningless, since the habitat diversity might be at least as important as the areas of the regions. Intriguingly, a comparison of New Zealand with the Andean páramo, discussed in §4*c*, suggests that there could be an area effect. The lack of a relationship might be because we do not have enough data points to separate area and habitat diversity effects (Kreft *et al.* 2008).

(c) *Regional analyses*

Although there is no strongly significant regional effect on the diversification rates in our data, there is an underlying regional pattern. Such regional patterns were already suggested by Ricklefs (2006*b*) for passerine birds.

(i) *Australia*

The rich Australian flora accumulated over the whole Neogene and may consist largely of slowly diversifying ancient lineages (figure 3). These can be described as mature radiations.

Crisp *et al.* (2004) have shown that many typical Australian clades date back to the Eocene, and the results here corroborate this. Elements of the Australian flora have been diversifying for a long time, possibly longer than most of those of other floras. Furthermore, there is no indication that these diversification rates have changed through time. The two recent and rapid radiations (in *Lepidium* and *Rytidosperma*) are questionable: Australian *Lepidium* may be of hybrid origin and thus, at least in part, polyphyletic (Mummenhoff *et al.* 2004), and the dating of *Rytidosperma* has not
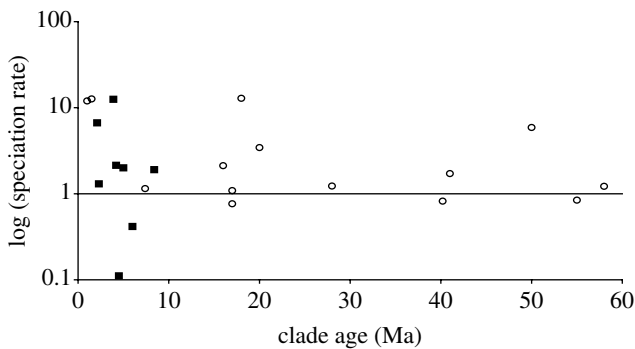
Figure 3. Australasian diversification rate mapped against clade age: open circles, Australian taxa; filled squares, taxa from New Zealand.
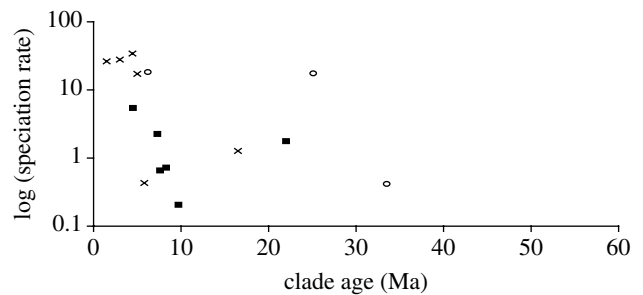

Figure 4. Neotropical radiations with the diversification rate mapped against clade age: crosses, Andean páramo taxa; filled squares, taxa from the Andean foothills; open circles, taxa from the lowlands.

yet been corroborated (Linder & Barker 2005). The diversification rates in Australia tend to be lower than those in the comparable Cape region, even though the geographical area is much bigger.

This long period of diversification might reflect the long-term geological stability in the smallest continent (Frakes 1999; Hill *et al.* 1999). There was very little uplift during the Tertiary, and much of the continent is peneplained to near sea level. Possibly linked to this geomorphological stability is climatic stability, at least along some coastal regions such as in Queensland or the southwestern tip of West Australia. The central portion of the continent has seen significant aridification (Crisp *et al.* 2001), however it has low diversity, and no clades in this investigation are centred in the arid region. Climatic change may have been gradual over tens of millions of years (Frakes 1999). The rich West Australian flora seems to have accumulated *in situ* through the Neogene, and so to have had a long local evolutionary history (Hopper & Gioia 2004), as exemplified in this analysis of *Banksia*.

(ii) *New Zealand*
In contrast to Australia, the modern species richness of the New Zealand flora appears to be the result of a number of recent radiations (McGlone *et al.* 2001), and in this analysis there are no New Zealand lineages older than 10 Ma (figure 3). This does not mean that there are no older lineages in New Zealand (see Lee *et al.* 2001); it merely means that the species-rich crown clades analysed are all relatively young, i.e. typical recent radiations. This relatively young age is consistent with the hypothesis that much of New Zealand was inundated during the Oligocene (Cooper & Millener 1993; Trewick & Morgan-Richards 2005), with the uplift of the mountains dated to *ca* 12 Myr ago and the alpine habitat dated only to the last 5 Ma (Chamberlain & Poage 2000). The climate change, from a warm and wet Miocene to cold and wet Pliocene (Trewick & Morgan-Richards 2005), added a further dynamic element into the New Zealand environment. This dynamism may have prevented the persistence of mature radiations with the consequent accumulation of diversity (Lee *et al.* 2001).

Analogous to the Andes, we see a flora that responded to the Pliocene uplift of higher mountains and the generation of montane and alpine habitats with a number of recent radiations, such as *Chionochloa* and *Hebe*. However, these recent radiations are less rapid than in the Andes (Mann–Whitney *U*-test, $p < 0.05$), which might be the result of the much smaller area in New Zealand (Ricklefs 2006b). Such recent alpine radiations have also been demonstrated for the fauna, and indeed, in general, the alpine biota of New Zealand is Pliocene in age (Buckley & Simon 2007).

This is in stark contrast to the mature radiations in neighbouring Australia. Possibly, if we had enough clades from the New Guinea uplands and New Caledonia, we might see a similar situation to New Zealand there (suggested by the radiation of *Nothofagus* and *Araucaria*; Setoguchi *et al.* 1998), indicating recent radiations along the periphery of the Australian plate, on newly exposed habitats (Ollier 1986; Murienne *et al.* 2005), while the central part of Australasia is largely stable and inhabited by mature radiations.

(iii) *Neotropics*
The extraordinary richness of the Neotropics reflects the presence of both recent and rapid radiations, as well as mature radiations (figure 4). The impact of the Andean orogeny on the diversification of the South American biota has been much investigated (see references in Brumfield & Edwards 2007). The uplift was initiated in the Early Miocene, *ca* 20 Myr ago (Burnham & Graham 1999), but 3000–4000 m high-elevation grassland (páramo, jalca and puna) dates from the Pliocene (Gregory-Wodzicki 2000).

The alpine páramo region is possibly the easiest to define. The region is home to recent and rapid radiations in *Lupinus*, *Gentianella* and *Valeriana*, and constitutes one of the most spectacular floral radiations (Hughes & Eastwood 2006). In addition to the taxa investigated here, possibly the largest radiation was in Ericaceae, with over 800 species (Luteyn 2002), and the most charismatic was *Calceolaria*, with 230 species. These clades responded to the new habitat with high diversification rates.

Much of the South American diversity is reported to be in the montane forests of the Andean slopes and foothills (Gentry 1982). Several slowly diversifying clades from the Andean foothills are included in this analysis. These include the large genus *Fuchsia*, which is associated with montane forest (Berry *et al.* 2004), and four small genera of the Annonaceae, the diversification of which is correlated with the uplift of the Andes (Pirie *et al.* 2006) in the Middle Miocene.
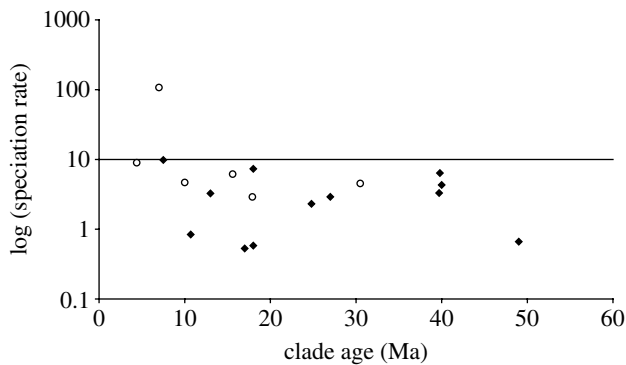
Figure 5. Cape radiations with the diversification rate mapped against clade age: filled diamonds, taxa with most species in the Cape Fold Mountains; open circles, taxa with most species in Namaqualand. However, there is substantial overlap between these two areas.

The presence of a large number of low-richness clades contributes to the richness, but there are also a number of recent and rapid radiations in the Andean foothills (Gentry 1982), exemplified here by *Inga* (Richardson et al. 2001a).

The lowland tropical radiation in *Guatteria* (Erkens et al. 2007) is puzzling, as this occurred in a relatively stable environment, with little evidence of dramatic climatic or geological changes during the Neogene. Furthermore, the genus is constituted of trees, rather than herbs or short-lived shrubs. Nevertheless, the genus groups with the Andean diversification as a recent and rapid radiation. Equally impressive is the Early Miocene (and so better described as mature) radiation of Annonaceae, which shows a similar speciation rate as *Inga* and *Guatteria*. A possible explanation for these high diversification rates could be sought in the very large area of available equatorial habitat in South America (more than the equatorial regions on the other continents; Young et al. 2002), as well as the wide range of habitats species from these genera were able to occupy in this region. The Andean uplift since the Miocene, by fragmenting distribution ranges and causing changes in rainfall patterns, may have stimulated the diversification of an already rich Neotropical lowland flora (Wilf et al. 2003; Jaramillo et al. 2006). The sampling of large Amazonian genera that are potential 'mature radiations' might be inadequate.

(iv) *Cape*

The remarkably rich Cape flora might be the result of a combination of mature radiations in the Cape Fold Mountains, as we well as recent and rapid radiations along the west coast (figure 5).

The Cape has long been regarded as one of the more remarkable radiation hotspots of the world's flora (Cowling et al. 1996; Cowling & Pressey 2001; Kreft & Jetz 2007), but the temporal progression of this radiation has been unclear. Initially, it was assumed that most of the radiations were initiated during the Late Miocene or Pliocene, coincident with a postulated climatic change (Linder et al. 1992; Richardson et al. 2001b), but molecular dating in the past few years indicates that the radiation of typical Cape clades was spread over much of the Neogene (Linder 2005). This

pattern is corroborated here: not only do the oldest crown groups date back to the Eocene, but also from the end Eocene some clades show above-average diversification rates. Since older clades are particularly sensitive to extinction episodes, this suggests that the flora has not suffered a severe extinction bottleneck. Much of this flora is restricted to the oligotrophic soils of the Triassic Cape Fold Mountains, a habitat that might pre-date the angiosperms (King 1963). The climate was also relatively stable; the region is wedged between two oceans. This geomorphological and climatic stability may have allowed the persistence of these older clades.

There is weak evidence for an accelerated diversification from the Late Miocene. This particularly affects the succulent clade Ruschioideae (Aizoaceae), which shows the highest diversification rate that has been documented (Klak et al. 2004). The other clades with high diversification are *Heliophila*, *Phylica* and *Pentaschistis*; with the exception of *Phylica*, these clades are well represented in the semi-arid west coast. A detailed investigation of the geographical patterns in the diversification of *Pelargonium* also indicated a rapidly radiating western clade nested within an older, slower diversifying eastern clade (Bakker et al. 2005). This indicates that while mature radiations are typical of the Cape Fold Mountains, recent and rapid radiations are more characteristic of the semi-arid west coast. The climate of this region is influenced by sea-surface temperatures, with lower temperatures associated with both a reduction in total rainfall, as well as an increase in summer aridity (Linder 2003; Dupont et al. 2005). There has been a gradual reduction in the sea-surface temperature along the South African west coast since the Middle Miocene, and this was dramatically accelerated in the Late Pliocene, coincident with the closing of the Panama seaway (Marlow et al. 2000; Dupont et al. 2005; Krammer et al. 2006). At the same time, during the Pliocene, there was renewed uplift of the eastern escarpment of Southern Africa (Partridge & Maud 2000), which blocked off more summer rain, thus also contributing to summer aridity along the west coast. The more rapid radiation of these clades could well reflect this availability of this new habitat (Klak et al. 2004).

(v) *Eurasia*

Like the tropical region, the Eurasian region is geographically extensive and includes several very diverse elements. The oldest radiation in the sample is the asteraceous Anthemideae, which radiated in the Mediterranean basin from *ca* 18 Myr ago (Oberprieler 2005). The dataset includes several more Mediterranean clades (*Thymelaea*, *Epimedium*); none of these have an above-average radiation rate. The Mediterranean served as a glacial refuge from which much of the central European flora was re-established (Hewitt 1999); it is therefore not surprising that such early diversity could survive in the region. The montane and alpine taxa of temperate Europe are all younger (*Globularia*, *Gentiana* sect. *Ciminalis*, *Soldanella*, *Primula* sect. *Auriculata*), but show above-average diversification rates, and can be regarded as recent and rapid radiations (Kadereit et al. 2004). This is somewhat

surprising, considering the extent of glaciations in these mountains during the Pleistocene, showing that diversification during periods of environmental instability may still be possible. However, the sample of taxa available from Eurasia is not adequate to analyse this complex area.

5. CONCLUSION

Our global analysis shows that the diversity in most clades rises very rapidly initially (first 2–8 Ma), after which the increase slows down. The early phase of the radiations, in which speciation dominates over extinction, can be classed as recent and rapid, while the later phase, in which extinction more or less balances speciation, can be classified as mature.

Recent and rapid radiations are largely dependent on new habitat or space becoming available. Typical of this pattern are the radiations in the Pliocene alpine habitats of the Andes and New Zealand's Southern Alps, and on the aridifying west coast of Southern Africa. This could be seen to be analogous to the ammonite radiations observed after mass extinction events (Stanley 1979). There are few or no recent and rapid radiations in old, stable environments, such as Australia or the Cape Fold Mountains. New habitats are necessary but not sufficient preconditions for radiations, and consequently not all clades in these new habitats radiate. Presumably taxon-specific attributes or key innovations are, additionally, required to trigger a radiation (as has been explored for angiosperms; Ricklefs & Renner 1994; Barraclough *et al.* 1998). We would also expect a certain time lag, and predict that the newly deglaciated habitats of the Northern Hemisphere, although being new habitats, should still do not have a rich endemic flora. Curiously, the highest endemism in Europe is in the previously glaciated alpine arc (Finnie *et al.* 2007), and genera such as *Carex* and *Astragalus* are very species rich. It would be nice to know whether 10 ka, 100 ka or 1 Ma are needed for diversification to become evident at species level. Most endemic species in deglaciated areas of Northern Eurasia are thought to have evolved after deglaciation, but are mostly polyploid hybrids (Brochmann *et al.* 2003), indicating that normal, diploid speciation needs at least 10 ka. Colonization might also play a significant role in stimulating diversification (Pennington & Dick 2004); it is possible that rapidly radiating clades came to their new habitats (dispersal), when compared with the perhaps more common situation where the habitats came to the clades (geotectonic/climatic change).

Mature radiations are the signature of the absence of dramatic extinction events during the Neogene. This does not mean that the extant species are necessarily ancient, but rather that lineage diversity has been accumulating for a long time—a species-rich clade, in which extinction balances speciation, remains species rich. The species richness can be consistent with a high turnover rate. Mature radiations are typically found tectonically stable areas (e.g. Australia, the Southern African coastal plain, the Amazon basin), which were not glaciated during the Pleistocene.

It is tempting to establish a link between the variation in species richness between different regions, and the patterns of diversification. To some extent, the patterns of diversification in each region are unique and were determined by local palaeoclimatic and geomorphological history. High diversity in a region can be the result of mature radiations (such as in Australia), recent and rapid radiations (such as the Andean páramo or New Zealand) or a mixture (such as the Cape or the Neotropics). This 'mixed model' appears to be responsible for the greatest regional species richness. Areas such as the Cape and the Neotropics might also harbour the highest lineage diversity, and thus provide the greatest diversity on the basis of which new radiations can be built. However, clades, and not biotas, radiate. An extrapolation from clades to biotas must be conditional, as there may be clades that do not fit the general pattern.

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