

When do plant radiations influence community assembly? The importance of historical contingency in the race for niche space

Andrew J. Tanentzap¹, Angela J. Brandt², Rob D. Smissen³, Peter B. Heenan³, Tadashi Fukami⁴ and William G. Lee^{2,5}

¹Ecosystems and Global Change Group, Department of Plant Sciences, University of Cambridge, Cambridge, CB2 3EA, UK; ²Landcare Research, Dunedin 9054, New Zealand; ³Landcare Research, Lincoln 7640, New Zealand; ⁴Department of Biology, Stanford University, Stanford, CA 94305, USA; ⁵School of Biological Sciences, University of Auckland, Auckland 1010, New Zealand

Author for correspondence:

Andrew J. Tanentzap

Tel: +44 1223 333 900

Email: ajt65@cam.ac.uk

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Summary

- Plant radiations are widespread but their influence on community assembly has rarely been investigated. Theory and some evidence suggest that radiations can allow lineages to monopolize niche space when founding species arrive early into new bioclimatic regions and exploit ecological opportunities. These early radiations may subsequently reduce niche availability and dampen diversification of later arrivals.
- We tested this hypothesis of time-dependent lineage diversification and community dominance using the alpine flora of New Zealand. We estimated ages of 16 genera from published phylogenies and determined their relative occurrence across climatic and physical gradients in the alpine zone. We used these data to reconstruct occupancy of environmental space through time, integrating palaeoclimatic and palaeogeological changes.
- Our analysis suggested that earlier-colonizing lineages encountered a greater availability of environmental space, which promoted greater species diversity and occupancy of niche space. Genera that occupied broader niches were subsequently more dominant in local communities. An earlier time of arrival also contributed to greater diversity independently of its influence in accessing niche space.
- We suggest that plant radiations influence community assembly when they arise early in the occupancy of environmental space, allowing them to exclude later-arriving colonists from ecological communities by niche preemption.

Introduction

New advances in macroevolutionary modelling, molecular phylogenetics, and the acquisition and sharing of past and present biodiversity data are improving our understanding of the processes through which species rapidly proliferate in diversity (Linder, 2008; Givnish, 2010; Linder *et al.*, 2014), but less thought has been given to the consequences of these radiations for the assembly of plant communities. Theory predicts that radiations should dominate ecological communities both in species number and in biomass when they are fitter than other taxa trying to occupy the same niche (Mayfield & Levine, 2010). One way in which fitness differences might emerge is through differences in initial population size. Lineages that arrive early into a new environment will have time to establish and spread as fully grown adults, placing later-arriving taxa at a considerable disadvantage in competing for resources (Silvertown *et al.*, 2005). Silvertown (2004) predicted that this ‘priority’ over the available environment and resources, which we define as niche space, also helps earlier arrivals to diversify,

further preempting the subsequent establishment of later-arriving taxa.

Evidence from some plant communities supports the prediction that earlier-arriving radiations should be more ecologically dominant (Lee *et al.*, 2012; Leopold *et al.*, 2015), but there is no consensus as to whether they are more diverse (Rabosky *et al.*, 2012) and thus better able to occupy niche space. We suggest that greater diversity within older lineages can arise in at least three ways. First, if diversification rates are relatively constant across clades, older lineages can be more diverse simply because they have had longer residence times – termed the ‘time-to-diversify hypothesis’ (Mittelbach *et al.*, 2007). Second, diversification can slow over time independent of niche dynamics, such as if there are concurrent changes in life-history traits or external factors that influence speciation and extinction (i.e. ‘time-dependent hypothesis’; Pyron & Burbrink, 2013; Moen & Morlon, 2014). For example, in animals, body size typically evolves to become larger and this can dampen rates of sympatry by increasing generation times (Etienne *et al.*, 2012a). Reduced climatic variability can similarly dampen the rate of

vicariance and subsequent range expansion that bring species back into sympatry (Weir & Schluter, 2004). Both examples can thus promote greater diversity in older lineages. Finally, older lineages can be more diverse if speciation slows and extinction accelerates because physical space and resources become utilized – known as the ‘niche filling hypothesis’ (Rosenzweig, 1975). Although the resulting dependence of diversification rates on species diversity is commonly reported (Pyrön & Burbrink, 2013), even after accounting for variation in extinction (Etienné *et al.*, 2012b), little is known about the underlying mechanisms (Rabosky, 2013). One potential mechanism for diversity dependence is that the range of concentrations of a limiting resource that new genotypes can use to avoid exclusion by resident species becomes smaller as new species join the community (Tilman, 1990), thereby reducing the probability that a nonwild-type individual will establish. Selection pressure to differentiate from resident species in the presence of limited niche space will further constrain biomass dominance and geographic range size in later arrivals, making them more difficult to isolate by vicariance and less likely to co-occur with older species through secondary sympatry (Pigot & Tobias, 2013). Smaller ranges can also limit occupancy of different habitats that impede gene flow (Anacker & Strauss, 2014), such as if flowering times are controlled locally by soil fertility (e.g. Savolainen *et al.*, 2006).

Ancestral species can also offset declines in available niche space where new traits or environments emerge that increase their fitness (Schluter, 2000; Klak *et al.*, 2004; Gavrillets & Vose, 2005; Hughes & Eastwood, 2006). These different ‘ecological opportunities’ typically favour greater trait variation across niche space and larger population sizes, both of which increase the susceptibility of populations to geographic isolation and select genotypes that are better adapted to a subset of habitats (Yoder *et al.*, 2010). Thus, lineages that occupy more available niche space should not only be more dominant, but also more diverse (Gehrke & Linder, 2011). Data supporting this idea may, however, depend on the primary mode of speciation. For taxa that diversify through allopatry, such as in environments that have been repeatedly isolated by geological and climatic activity (Winkworth *et al.*, 2005; Heenan & McGlone, 2013), occupancy across a greater range of niche space may promote speciation by increasing the probability that a subset of individuals become isolated, while the reverse may be true where parapatry is more common because gene flow is easier to maintain among populations (Birand *et al.*, 2012).

Here, our aim is to integrate the different hypothesized interactions among evolutionary time, niche occupancy, and ecological opportunity into a single testable model that predicts when diversification has consequences for plant community assembly. We specifically test the predictions that earlier-colonizing radiations encounter: (1) a greater availability of environmental space at the time of their arrival into a new bioclimatic region, promoting *in situ* diversification (measured as number of species per genus), and that this (2) leads to a positive association between within-clade species diversity and niche occupancy, which (3) favours community dominance of these older radiations

(Fig. 1a). We expect that this sequence of events arises because niche space is progressively filled over time (Fig. 1b), although our model allows for time-dependent effects independent of niche dynamics. Later-arriving lineages can therefore occupy only the relatively small proportion of total niche space that remains available, limiting their potential for diversification (Fig. 1c). Throughout, we do not try to identify the exact mechanism of diversification, which can arise through greater allopatric, peripatric, parapatric, or sympatric speciation associated with larger niche breadth and population size (Pigot & Tobias, 2013; Anacker & Strauss, 2014), or with less extinction under these conditions. Our only explicit consideration of speciation mechanisms is allowing the variation in niche occupancy that each lineage experiences through time to influence diversity. We might expect, for example, that lineages experiencing more expansion and contraction (i.e. greater variation) will be more likely to form isolated populations that differentiate into new species (Wilson, 1959; Winkworth *et al.*, 2005; Price *et al.*, 2014). We also test the importance of a lineage’s prehistory. One hypothesis is that traits that allow ancestral species to access future opportunities more readily, such as being closer in environmental space to sites they invade, can hasten niche occupancy (Harvey & Rambaut, 2000; Fig. 1d). However, this may not necessarily promote *in situ* diversification. Ancestors with environmental requirements that closely match their new niches could suppress the growth of new genotypes and experience weak selection to shift to new traits that promote diversification (Knape *et al.*, 2012; Fukami, 2015).

Our focus is on the New Zealand alpine zone, which offers a model for studying plant radiations. This bioclimatic region has 53 highly diverse genera (≥ 10 species throughout New Zealand), many of which are monophyletic and established with the uplift of the Southern Alps from about the late-Miocene onwards (Winkworth *et al.*, 2005; Heenan & McGlone, 2013). Several lineages also predate the formation of cool open habitats, allowing us to test the importance of preadaptations and geoclimatic variation for niche filling and eventual community dominance. We worked within this system by sampling vegetation above the natural treeline in 258 plots across an entire mountain range and reconstructing the extent of above-treeline habitats in this region during the last 20 million yr from proxies of palaeoclimate and mountain summit height. We then used these data to estimate the interactions among environmental occupancy, diversification, and community dominance throughout evolutionary time for 16 genera that are characteristic of the alpine zone. These focal genera cover a range of functional and life-history strategies (Table 1). Previously, we found that earlier-arriving lineages dominated plant communities (Lee *et al.*, 2012), and that this pattern varied with local environmental conditions (Leopold *et al.*, 2015). We now build on these findings by using an explicit model of temporal niche dynamics to test a general hypothesis that predicts when plant radiations emerge and influence community dynamics (Fig. 1). Our findings point to the importance of priority effects in allowing species to exploit opportunities that promote evolutionary radiations and ecological dominance.

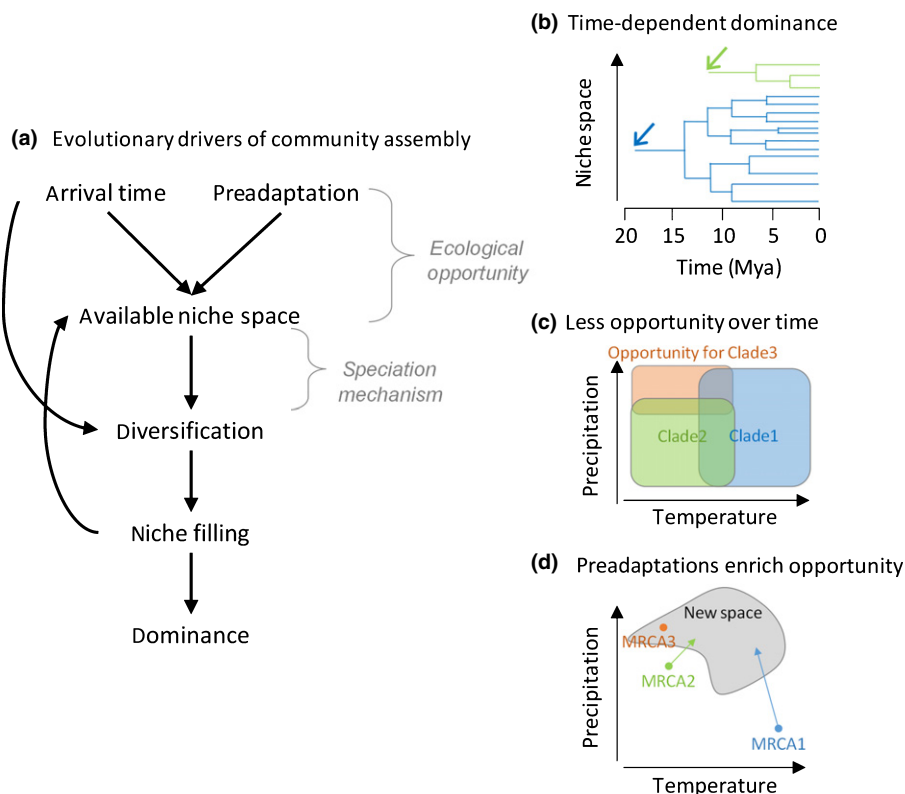


Fig. 1 Hypothesized model of how priority effects can drive diversification of early-arriving taxa, excluding later-arriving species by occupying niche space. (a) Schematic of drivers predicted to influence community assembly. (b) Predicted diversification across niche space. Arrows indicate time of ancestor immigration for each of two lineages. (c) Less ecological opportunity is available for later-arriving species as earlier-arriving species diversify and fill niche space. (d) Ancestral species, denoted by points MRCA1, 2 and 3, will invade new opportunities that are closer to them in niche space, here defined by precipitation and temperature gradients (Harvey & Rambaut, 2000). This may explain why MRCA2 can find space in which to diversify despite arriving after MRCA1 (see b). Alternatively, species that are already adapted to the new opportunity, such as MRCA3, may experience little selective pressure to shift their environmental occupancy. Consequently, MRCA3 may not diversify extensively, particularly if it is already on or near an adaptive peak (Knape *et al.*, 2012).

Table 1 Species diversity and environmental occupancy of 16 genera within the Murchison Mountains, New Zealand

| Genus | Family | Stem age | Life form | Ancestral habitat | No. of species | % of plots | <i>o</i> |
|----------------------|----------------|------------|-----------|-------------------|----------------|------------|----------|
| <i>Abrotanella</i> | Asteraceae | 6.4 (1.4) | Forb | Above | 4 (10) | 9.3 | 0.02 |
| <i>Aciphylla</i> | Apiaceae | 8.4 (2.6) | Forb | Above | 7 (42) | 45.7 | 0.45 |
| <i>Anisotome</i> | Apiaceae | 11.1 (3.3) | Forb | Above | 6 (15) | 84.9 | 0.89 |
| <i>Astelia</i> | Asteliaceae | 9.1 (3.1) | Forb | Below | 4 (13) | 49.6 | 0.49 |
| <i>Chaerophyllum</i> | Apiaceae | 1.6 (0.5) | Forb | Above | 1 (4) | 11.2 | 0.07 |
| <i>Chionochloa</i> | Poaceae | 20.0 (1.9) | Gram | Below | 8 (23) | 96.5 | 1.00 |
| <i>Craspedia</i> | Asteraceae | 3.1 (0.6) | Forb | Above | 2 (7) | 17.4 | 0.12 |
| <i>Dracophyllum</i> | Ericaceae | 6.8 (1.5) | Woody | Below | 7 (37) | 70.9 | 0.97 |
| <i>Euphrasia</i> | Orobanchaceae | 5.7 (0.7) | Forb | Below | 5 (16) | 18.6 | 0.12 |
| <i>Forstera</i> | Stylidiaceae | 6.3 (1.1) | Forb | Above | 3 (8) | 62.4 | 0.44 |
| <i>Gentianella</i> | Gentianaceae | 2.1 (0.6) | Forb | Above | 5 (30) | 53.9 | 0.60 |
| <i>Oreobolus</i> | Cyperaceae | 5.1 (0.9) | Gram | Above | 3 (3) | 35.7 | 0.33 |
| <i>Plantago</i> | Plantaginaceae | 1.6 (0.4) | Forb | Above | 2 (11) | 29.8 | 0.24 |
| <i>Ranunculus</i> | Ranunculaceae | 5.1 (0.9) | Forb | Below | 6 (44) | 32.2 | 0.32 |
| <i>Veronica</i> | Plantaginaceae | 9.7 (2.6) | Woody | Below | 10 (127) | 74.0 | 0.85 |
| <i>Wahlenbergia</i> | Campanulaceae | 4.8 (1.5) | Forb | Below | 1 (11) | 7.8 | 0.02 |

For each genus, the mean stem age (million yr) was estimated from existing studies (see Supporting Information Table S1); SD is in parentheses. We also report the life form (graminoid, forb, woody-stemmed), ancestral habitat (above or below the treeline), number of unique species recorded in the data set (and New Zealand as a whole, in parentheses; after <http://nzflora.landcareresearch.co.nz/>), proportion of study plots in which each genus occurred, and relative niche occupancy (*o*).

Materials and Methods

Study genera

We focused our analysis on 16 widely distributed genera for which time-calibrated molecular phylogenies have been published (Table 1). Immigration timing of ancestral species into New Zealand cannot be known exactly. Thus, estimates of the age of divergence between the most recent common ancestor of a New Zealand clade and its nearest extant relative outside of New Zealand were used as the best available estimates of lineage ages (i.e. stem ages). If the New Zealand representatives of a genus did not form a monophyletic group, such as if there were two independent colonizations, we took the stem age of the oldest clade. We compiled estimates of these ages and their associated uncertainty from published sources that used a variety of gene regions and molecular clock methods (see Supporting Information Table S1). For sources reporting 95% highest posterior density intervals, we estimated a variance using the longer of the two tails and assuming a normal distribution around the mean (after Lee *et al.*, 2012). We did not use age of the most recent common ancestor of the New Zealand clade (i.e. crown age) in our analyses, as this simply captures when a lineage started diversifying and ancestors may have arrived long before this started (Pirie *et al.*, 2010). Estimates can also vary systematically over time if environmental changes trigger shifts in diversification rates in later arrivals, for example if new habitat is created. Irrespective of this, crown age was strongly correlated with our inferred arrival date for the 10 lineages for which both estimates were available ($r = 0.81$; $P = 0.008$).

Vegetation and environmental data

We collected vegetation data across the alpine zone of the Murchison Mountains, South Island, New Zealand (760–1620 m above sea level (m asl), 45°15'S, 167°33'E). The mountain range covers 512 km² and spans two distinct environmental gradients. The first is a strong east-to-west rainfall gradient of *c.* 2500–5000 mm yr⁻¹, and the second is a temperature gradient associated with increasing elevation. Mean annual temperatures at 890 m asl have averaged 5.3°C between 1973 and 2013 and decline by 0.98°C per 100 m elevation gain (Tanentzap *et al.*, 2012). Vegetation is dominated by a band of low scrubland that transitions into snow tussock (*Chionochloa* spp.) grasslands at *c.* 1100 m asl, until being replaced by alpine fellfield on the mountain tops at *c.* 1430 m asl.

Across the entire range, we positioned 258 5 × 5 m plots at *c.* 100 m elevation intervals along 67 randomly placed transects. The total percent cover for each of 282 vascular plant species was visually estimated in each plot. From these data, we calculated two measures of community dominance: relative generic abundance (*A*), defined as the percent cover of a focal genus divided by the summed percent cover of all other species in a plot, and relative generic richness (*R*), which was the number of species of a focal genus divided by the number of all other species in a plot (Leopold *et al.*, 2015).

We used species occurrences to estimate the occupancy of each genus in environmental space. We defined occupancy in terms of physical and climatic variables that have an explicit physiological role in influencing New Zealand plant distributions: annual average of the monthly ratios of rainfall to potential evaporation (i.e. water balance), annual solar radiation, slope, aspect, mean annual air temperature (MAT) and shortest distance to coastline (DTC). All environmental data were extracted from the Land Environments of New Zealand (LENZ) database (Leathwick *et al.*, 2003). We interpreted MAT as an indicator of potential cold limitation, as it correlated strongly with minimum air temperatures of the coldest month across our study plots (Spearman's rank correlation, $\rho = 0.99$, $P < 0.001$). DTC was considered to be an indicator of continental vs maritime climate influence rather than an absolute measure of precipitation or seasonality. Before analyses, values of MAT were linearly transformed to the distance that each plot was located above the treeline (DAT), in order to consider more explicitly whether preadaptation to non-forested habitats promoted access to niche space and community dominance in the alpine zone. The transformation involved dividing the difference between MAT of each plot and that at which treeline forms in New Zealand, taken as 5.55°C (Cieraad & McGlone, 2014), by the adiabatic lapse rate.

For each genus *i*, we calculated present-day niche occupancy o_i in the Murchison Mts as the volume of a convex hull around observations of its presence along the six environmental gradients (Cornwell *et al.*, 2006). Multiple species can overlap across this space, making the maximum size of environmental space equal to the product of the convex hull volume across all environmental observations and the maximum number of species that co-occur at a single observation of these variables (i.e. plot) – equal to 14 in our dataset. Past estimates of environmental occupancy were derived only from MAT and DTC because we could not reconstruct other bioclimatic and physical variables through the changing geomorphological history of New Zealand. Reassuringly, o_i remained relatively unchanged when estimated solely from DTC and DAT as compared with all six of the environmental predictors ($\rho = 0.98$, $P < 0.001$).

Palaeoreconstruction of environmental space

In order to estimate the availability of environmental space through evolutionary time, we first reconstructed DAT by inferring MAT from measurements of $\delta^{18}\text{O}$ in planktonic foraminifera deposited in ocean sediment cores. This involved applying standard equations to reconstruct the chronology of sea surface temperature (SST) directly offshore of South Island (see Methods S1 for details). Linearly interpolating between data points then allowed us to estimate SST at the arrival time of each genus (Fig. 2a). We subsequently transferred oceanic measurements to land using the predicted relationship between MAT in the Murchison Mts from 1982 to 2013 and SSTs at the nearest point to each of the ocean core sites only 14–15 km away. Modern SSTs were obtained at a daily resolution from the National Oceanographic Data Centre (www.ncdc.noaa.gov) and averaged in each year. The linear model that we used for all predictions until 18.8

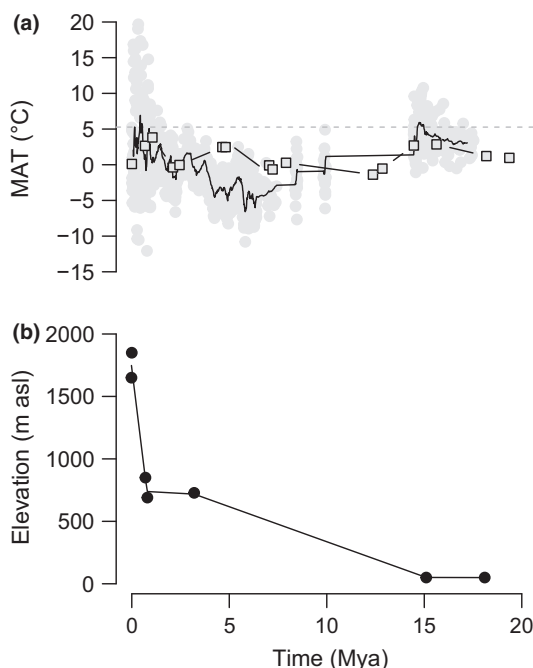


Fig. 2 Palaeoreconstruction of environmental space in the Murchison Mountains, New Zealand. (a) Mean annual temperature (MAT) predicted at 890 m above sea level (m asl) from sampling of planktonic foraminifera in marine sediments off eastern South Island (circles) and southern Tasmania (squares). The solid line is the 25-point moving average through the eastern South Island core used to interpolate sea surface temperature (SST) up until 18.8 million yr ago (Mya) (Supporting Information Methods S1). The dashed grey line is the mean of MAT from 1973 to 2013. (b) Maximum elevation predicted from mean (U-Th)/He apatite date of rocks collected at different elevations. The line is a cubic smoothing spline fitted through the points.

million yr ago (Mya) explained a relatively high amount of variation in land-based MAT ($R^2 = 0.60$; $R^2 = 0.32$ for model used for predictions between 18.8 and 20.0 Mya; Fig. S1). Oceanic fronts surrounding the New Zealand mainland have been relatively stable over the past 20 million yr, following the opening of the Drake Passage and restriction of the Indonesian gateway (Nelson & Cooke, 2001), supporting our efforts to link SST with land MAT over this period.

Elevation has also changed over time, coinciding with the uplift of the Southern Alps, so estimates of MAT generated for the Murchison Mts weather station at 890 m asl need to be corrected with the adiabatic lapse rate. Measurement of $\delta^4\text{He}$ produced from the decay of Ur and Th within minerals such as apatite offer one approach for inferring the age and rate of rock uplift from the Earth's surface. Here we used 12 (U-Th)/He apatite dates collected from around the Murchison Mts to derive a profile of cumulative elevation through time, averaging ages taken at the same elevation (Sutherland *et al.*, 2009). We took the age of the maximum elevation in the Murchison Mts (1850 m asl) as being present day and subtracted the amount of time that uplift would have been offset by denudation from the (U-Th)/He dates, which we inferred from the age of samples at 0 m asl (= 1.9 million yr). Uplift itself was considered to have initiated 17 Mya in the Murchison Mts (Sutherland *et al.*, 2009) and

we set an initial surface elevation of 50 m (see Methods S1 for full discussion). Linear interpolation on a cubic smoothing spline fitted among data points allowed us to estimate the maximum elevation at the arrival time of each genus (Fig. 2b). The corresponding elevation of the Murchison Mts weather station was then scaled relative to this value to correct MAT.

Given palaeo-MAT, available niche space at the arrival time of each genus was calculated as the total extent of environmental space (E_{max}) minus the potential space occupied by prior arriving genera (E). E_{max} was simply the convex hull volume around all plots, as for the present day (see earlier text), but using a palaeo-DAT, generated by correcting palaeo-MAT for the palaeo-elevation of each of the 258 study plots. Study plots will also have overlapped with different parts of each genus's niche as climate has changed over time (Fig. S2). As the niche space of each genus will be much broader than presently observed in the Murchison Mts (Fig. S2), we estimated a 'fundamental' niche by collating geographic coordinates from an additional 18 140 occurrences throughout the whole of New Zealand for the specific species found in the Murchison Mts. Data were downloaded from the Global Biodiversity Information Facility (www.gbif.org) and intersected with the LENZ database to derive DAT and DTC. We then calculated E at each time point as the summed volume of intersection between the space used to derive E_{max} and each of the fundamental niches of prior arrivals. We discuss the assumptions underlying this approach in Methods S1.

We acknowledge that reconstructing the dynamics of species niches is very difficult for the long timescales studied here. The clear and rationalized palaeoclimate and geomorphological scenario we develop provides one of the few approaches presently possible for inferring palaeoniches. In general, our scenario is consistent with patterns observed from different proxies elsewhere (see Methods S1 for a full discussion). Future extensions in the temporal window of palaeoclimate models may make these exercises easier.

Test of time-dependent interactions among niche occupancy, diversification and dominance

We tested whether earlier-arriving genera had more available niche space, leading to lineage diversification that filled niche space and dominated ecological communities, as predicted in Fig. 1(a). Our approach used Bayesian hierarchical modelling to test our presumed causal network of interactions (after Tanentzap *et al.*, 2014).

We first expressed the available environmental space a_i observed at the time of colonization by each genus i as the difference between the total size of environmental space $E_{\text{max},i}$ and the potential space occupied by all other older genera E_j when the genus i is presumed to have colonized. Of course, this does not mean that all niche space is available for the oldest genus, just that there is more relative to other genera in our study. E_{max} has also increased over time with the creation of topography (Fig. 2b), so earlier-arriving genera did not access a greater extent of space simply because of environmental changes. We then predicted a_i for each genus i from the time when the lineage

colonized New Zealand, t_b and whether it was derived from an alpine habitat (Table 1). Genera were classified as ancestrally present or absent above the treeline using parsimony optimization that considered the least inclusive clade containing all New Zealand species and its nearest sister clade, based on published phylogenies. The most parsimonious outcome for a sister clade with species above and below the treeline was to select the former as the ancestral state, but this was only an issue for *Gentianella* given the outgroups that we used. Occurrence data to inform the reconstruction were taken from floras (mainly Mark, 2012) and the Global Biodiversity Information Facility. We also allowed access to environmental space to vary with the type of life form (i.e. graminoid, forb, or woody-stemmed; see Table 1). Finally, earlier-arriving genera may access more available space than later arrivals because they overlap more with the species present at the time of their arrival (i.e. niche packing, g_i). We accounted for this by deriving g_i as the maximum volume of intersection between the fundamental niche of genus i and each prior arrival. For *Chionochloa*, the first arrival, g_i was equal to the minimum observed value, as other plants were certainly present at the time of its arrival. We allowed the effect of g_i to vary among life forms, such as if some groups were better at packing into environmental space than others. For example, woody-stemmed species may utilize more vertical space and so exhibit greater niche overlap. Values of a_i were assumed to be normally distributed and we fitted the following model to the observations:

$$a_i \sim N(\mu_i^{(1)}, \sigma_i^{(1)})$$

$$\mu_i^{(1)} = \alpha^{(1)} + \beta_1 \log_e(t_i) + \eta_i^{(1)} + \gamma_{i[k]}^{(1)} + \beta_2 g_i, \quad \text{Eqn 1}$$

where $\alpha^{(1)}$ is the estimated mean a_i for genera with nonalpine (i.e. below treeline) ancestors and graminoid life forms, β_1 is the effect of lineage age, $\eta_i^{(1)}$ is the estimated change in $\alpha^{(1)}$ associated with an alpine ancestral habitat, $\gamma_{i[k]}^{(1)}$ is the estimated change in $\alpha^{(1)}$ associated with the k th nongraminoid life form, and β_2 is the effect of packing. We propagated uncertainty associated with mean estimates of t_i into Eqn 1 as: $\sigma_i^{(1)} = \sqrt{(\beta_1 \tau_i / t_i)^2 + \sigma^{(1)2}}$, where τ_i and $\sigma^{(1)}$ are the observed SD for each genus i derived from published studies and an estimated residual SD, respectively.

We then predicted the number of species in our study plots, s_i , for each genus i given a_i . This analysis tests the idea that species that are able to access a broader environmental space are more susceptible to allopatric speciation, such as through vicariance (Pigot & Tobias, 2013), or parapatric speciation, such as through variation in gene flow (Anacker & Strauss, 2014). The analysis, however, does not assume a specific diversification mechanism. We also tested how diversity varied with both the effects of time, independent of its role in enabling access to niche space t_i' , and temporal variation in niche occupancy (v_i), such as from changing climatic or geological conditions in our study region (Winkworth *et al.*, 2005). We calculated t_i' by removing the variation in lineage age, $\log_e(t_i)$, that was linearly associated with access to niche space a_i . v_i was equal to the coefficient of variation calculated from the niche occupancy of each genus i over 25

equally spaced intervals from the time of its presumed colonization until the present day. We assumed that s_i was drawn from a Poisson distribution to account for count data and modelled values as:

$$s_i \sim \text{Pois}(\lambda_i)$$

$$\log_e(\lambda_i) = \alpha^{(2)} + \beta_3 a_i + \beta_4 t_i' + \beta_5 v_i, \quad \text{Eqn 2}$$

$$t_i' = \log_e(t_i) - \beta_6 a_i,$$

$$t_i \sim N(e^{\beta_6 a_i}, \tau_i \sigma)$$

where $\alpha^{(2)}$ is the mean s_i and σ is estimated.

We used the same formulation as Eqn 2 to predict the environmental space, o_i , that each genus presently occupied given their different richness, s_i and residence time, t_i but allowed values to be normally distributed:

$$o_i \sim N(\mu_i^{(2)}, \sigma^{(2)} \Sigma)$$

$$\mu_i^{(2)} = \alpha^{(3)} + \beta_7 s_i + \beta_8 t_i' + \beta_9 \log_e(f_i), \quad \text{Eqn 3}$$

where f_i is the observed number of plots in which a genus occurs relative to its richness and accounts for the fact that convex hull volumes will be larger as species within a genus are more abundant, that is, removes variation in o_i resulting from filling of geographic space. We allowed f_i to be nonlinearly associated with o_i as might be expected if increasing frequency has little additional effect on occupancy once a genus is widespread. Environmental occupancy can also be more similar among more closely related species (e.g. Anacker & Strauss, 2014), such as if it were strongly evolutionarily conserved. We accounted for this nonindependence by expressing o_i as a function of a variance-covariance matrix Σ , derived from assuming that the expected covariance in o_i between any two genera was proportional to their shared evolutionary history along a phylogenetic tree. We estimated a phylogeny for our focal genera from a standard DNA marker used to resolve evolutionary relationships at higher taxonomic levels with MrBayes 3.2 (Huelsenbeck *et al.*, 2004); full details are given in Methods S2 and Table S2. We then scaled Σ by an estimated SD $\sigma^{(2)}$.

Finally, we predicted the community dominance of each genus i in each plot j given o_i the type of life form and its prehistory, allowing for unexplained plot-level variation ε_j :

$$A_{ij} \sim \log_e N(\mu_{ij}^{(3)}, \sigma_i^{(3)})$$

$$\mu_{ij}^{(3)} = \alpha^{(4)} + \beta_{10} o_i + \gamma_{i[k]}^{(2)} + \eta_i^{(2)} + \varepsilon_j, \quad \text{Eqn 4}$$

where $\alpha^{(4)}$ is the mean relative generic abundance A_{ij} , β_{10} is the estimated effect of o_i and ε_j is drawn from a normal distribution with estimated SD. We refitted Eqn 4 to predict relative generic richness R_{ij} but allowed for this value to differ among genera simply because they differed in species richness by adding $\beta_{11} s_i$ to Eqn 4 and removed the genus-level estimate of residual variance; it was included for A_{ij} to eliminate heteroskedasticity.

Modelling approach

We fitted all our models at once using Markov chain Monte Carlo (MCMC) sampling by calling Stan v.2.5 (Stan Development Team, 2014) from R v.3.0 (R Development Core Team, 2013). Four MCMC chains of 3000 iterations were simulated with a burn-in of 2000 runs. We assigned uninformative priors for all regression coefficients (i.e. α , β , η , γ) and SDs (i.e. σ) that were $\sim N(0, 100)$ and $U(0, 100)$, respectively. We sampled ϵ' from posterior distributions that were estimated separately from Eqns 1–4 to avoid feedback influencing the resulting values.

Effects for all parameters were inferred by calculating posterior means and 95% credible intervals (CIs) from a subset of 1000 simulations, and supported our study predictions in Fig. 1(a) if they were positive and excluded zero. We also standardized all predictors to a mean of 0 and an SD of 1 so that their estimated effects represented the change in the response with a 1 SD change in the predictor. The proportion of variance explained by all predictor variables at the level of our measured data (including plot-level variation where applicable) was summarized with a Bayesian R^2 (Gelman & Hill, 2007).

Results

Dominance is an outcome of time-dependent diversification and niche occupancy

We found support for all three of our central predictions (Fig. 3). First, the greater availability of environmental space encountered by earlier-arriving lineages was associated with a higher species richness within genera (95% CI for unstandardized effects β_1 and β_3 : 0.11–0.57 and 0.24–0.93, respectively; Fig. 4a,b). Preadaptation had little influence on access to this space and subsequent levels of diversity. Lineages with alpine ancestors encountered as much available niche space as genera from nonalpine habitats (95% CI for $\eta^{(1)}$: –0.25–0.49), and there was no difference in the availability of environmental space for different life forms (95% CIs for $\gamma^{(1)}$: –0.43–0.50 and –0.53–0.67 for forbs and woody species, respectively). Increasing the maximum amount of overlap among genera similarly did not promote additional access to environmental space (95% CI for β_2 : –0.12–0.34). Instead, greater packing was associated with genera that occupied less environmental space in the present day ($\rho = -0.57$, $P = 0.020$), suggesting that it represented an outcome of an environment crowded with more species and that filling of niche space by earlier arrivals was driven by greater occupancy rather than packing.

Second, genera with greater species diversity occupied more environmental space, as expected where they radiate into niche space (95% CI β_7 : 0.23–0.40; Fig. 4c). This effect was stronger than that of lineage age when we removed variation in arrival time associated with niche occupancy (95% CIs for β_8 : –0.07–0.11; β_7 – β_8 : 0.15–0.43). The lack of an association between lineage age and environmental occupancy did not support the idea that older monotypic genera could be dominant simply because they have had more time to expand their

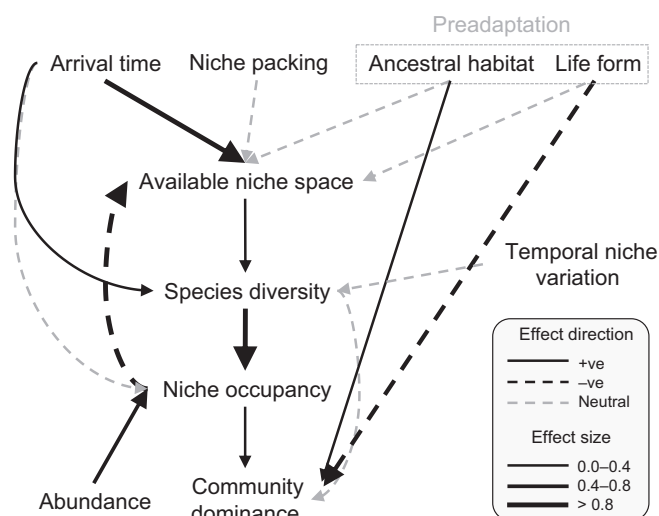


Fig. 3 Modelled network of dependencies among characteristics of 16 alpine plant radiations. Arrows point at modelled variables, with mean effects of one variable on another described in the key. Effects were standardized to represent the proportion of a SD in the response that changes with 1 SD in an associated predictor so as to be directly comparable across models. Negative effect of life form indicates that nongraminoids are associated with lower dominance. Environmental space occupied by each genus, o_i , will influence the relative availability of $\sum_{k=i}^{k=i} o_k$ environmental space for subsequent colonists $a_{(i+1)}$ as $a_{(i+1)} = 1 - \sum_{k=1}^{k=i} o_k$, by definition, and thus the change in $a_{(i+1)}$ with o_i will be $\partial a_{(i+1)} / \partial o_i = -1$. SD and random effects (i.e. σ and ϵ , respectively) are omitted for clarity. Bayesian R^2 for models ranged between 0.41 and 0.80.

habitat range, and genera with more abundant species irrespective of their age had a greater environmental occupancy (95% CI β_9 : 0.09–0.27).

Finally, we found that genera that occupied a greater portion of niche space were more dominant within our vegetation plots (Fig. 5). Both relative generic abundance and relative generic richness increased with the volume that genera occupied along our environmental axes (95% CIs for β_{10} on log-scale: 0.61–0.76 and 0.12–0.17, respectively). For both measures, forbs and woody species had a lower mean dominance than graminoids (95% CIs for $\gamma^{(2)}$: –2.15–0.10 and –2.08–0.34, respectively), although this was probably because the two graminoids in our study, *Chionochloa* and *Oreobolus*, arrived relatively early and were able to occupy niche space more fully (Table 1). Genera derived from above-treeline ancestors were also more dominant in terms of ground cover and species richness (95% CIs for $\eta^{(2)}$: 0.56–0.93 and 0.09–0.17, respectively), and the richness dominance of genera did not increase with species richness of the lineage (95% CI for β_{11} : –0.01–0.04). All parameter estimates are reported in Table S3.

Time-dependence independent of niche dynamics

We found support for the role of time in promoting diversification, but not climatic variation experienced by our focal genera over the last 20 million yr. In addition to accessing more space, older lineages were more diverse as a result of longer residence

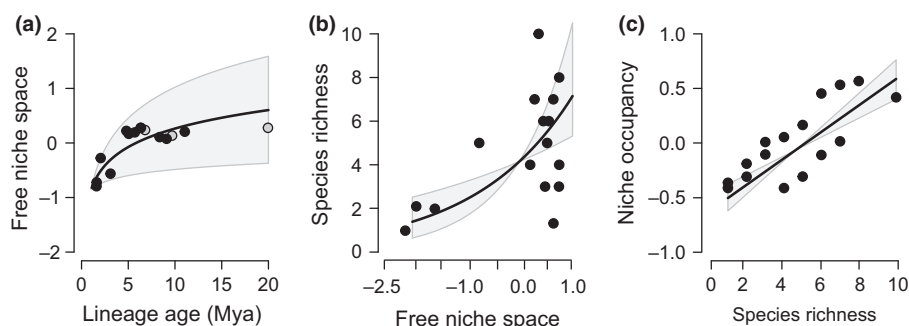


Fig. 4 Time-dependent niche filling drives diversification and subsequent niche occupancy in 16 New Zealand plant genera. (a) Earlier-arriving (i.e. older) genera access more free environmental space; (b) greater access to environmental space is associated with greater species diversity of each genus; and (c) greater species richness promotes greater niche occupancy. Niche space is defined by positions of species along six biologically relevant physical and climatic gradients. Measures of niche space and occupancy do not consider lineages arriving into New Zealand before those that we are studying and so are presented as relative values that were scaled to a mean of zero for interpretation. Solid lines are mean model fits \pm 95% credible intervals (CIs) in grey. In (a), model fit is shown for forbs (black circles), with graminoid and woody genera plotted in grey.

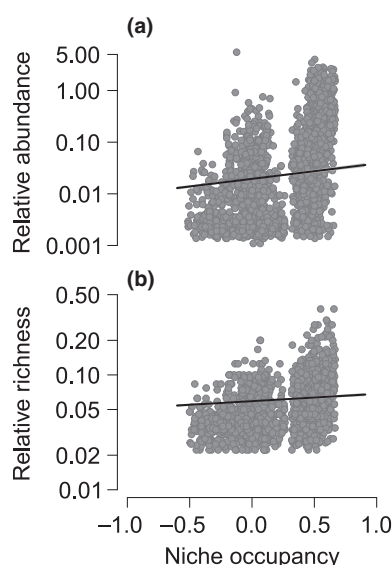


Fig. 5 Community dominance increases with niche filling, defined by positions of genera along six biologically relevant physical and climatic gradients. Points are either relative generic abundance (a) or relative generic richness (b) in each of 258 plots; not all genera were present in all plots (total $n = 1806$). Niche occupancy is dimensionless and so was scaled to a mean of zero for interpretation. Solid lines are mean model fits \pm 95% credible intervals (CIs) for forbs with alpine ancestors, which were the most common genera (Table 1).

times, once we accounted for the association between arrival time and niche availability (95% CI for β_4 : 0.02–0.50). The strength of this effect was as important as that of access to niche space (95% CI for $\beta_4 - \beta_3$: –0.63–0.05). By contrast, although the relative variation in climate experienced by each genus has declined over time ($r = 0.62$, $P = 0.010$), this could not explain the lower species richness of younger clades (95% CI for β_5 : –0.47–0.12). These results lend support to a time-to-diversify mechanism and suggest that time-dependent processes other than changes in climatic variation could matter, or their effects in reproductively isolating populations could depend on genus-specific life history traits.

Discussion

Our study suggests that earlier-arriving lineages influence community assembly when they have priority over niche space and diversify within it to limit the establishment of later-arriving colonists. This result empirically supports Silvertown's (2004) hypothesis for niche preemption limiting the diversification of late-arriving lineages. Our findings also extend Silvertown (2004) and our previous work (Lee *et al.*, 2012; Leopold *et al.*, 2015) to suggest that time-dependent niche occupancy interacts with diversification to influence community assembly. As species in many plant radiations across the world's bioclimatic zones have emerged over millions of years, even in relatively recent (post-Miocene) diversification episodes (Linder, 2008; Madriñán *et al.*, 2013), our results also offer a potential mechanism to explain biodiversity patterns elsewhere. The model of how environmental occupancy, preadaptation, diversification, and community dominance interact (Fig. 3) is consistent with many studies reporting that community dynamics are influenced by immigration history and the timing of speciation (Fukami *et al.*, 2007; Lee *et al.*, 2012; Waters *et al.*, 2013; von Gillhaussen *et al.*, 2014). Of course, historical processes cannot be unequivocally identified only with phylogenetics and climatic reconstructions, and the correlative evidence that we find – albeit in the context of a presumed causal network of interactions – is consistent with a variety of potential processes that we discuss below.

Radiations arise from time-dependent access to niche space

Our findings support the idea that diversification is more widespread in earlier-arriving genera because they have had more time to accumulate broader niches that favour allopatric speciation mechanisms (Yoder *et al.*, 2010). In New Zealand, geographic and climatic barriers would have reproductively isolated earlier-arriving and more widely ranging species repeatedly through evolutionary time (Winkworth *et al.*, 2005; Heenan & McGlone, 2013). Lockhart *et al.* (2001) suggested that this was a mechanism by which *Ranunculus* has diversified into species and genetically distinct populations that are restricted to

different geographic regions. Subsequent dispersal and niche expansion might have brought these species back into contact (Wilson, 1959; Winkworth *et al.*, 2005; Price *et al.*, 2014), resulting in co-occurring sister taxa today, as observed in our plots for pairs such as *Forstera sedifolia* and *Forstera tenella* (Wagstaff & Wege, 2002), *Oreobolus pectinatus* and *O. strictus* (Chacón *et al.*, 2006), and several *Chionochloa* spp. (Pirie *et al.*, 2010). Gehrke & Linder (2011) speculated that a similar process of past allopatric speciation could explain the greater diversity of older lineages along the isolated mountaintops of sub-Saharan Africa. Older lineages would have had more time to occupy a greater range of sites, including those distant from source populations, making them more susceptible to isolation (Gehrke & Linder, 2011).

Other mechanisms aside from allopatric speciation remain compatible with our model of time-dependent lineage diversification. For example, earlier-arriving genera reaching a greater range of habitats may be more likely to experience divergent selection on ecological and/or reproductive traits that promote speciation events within the range of ancestors (van der Niet & Johnson, 2009; Anacker & Strauss, 2014; Grossenbacher *et al.*, 2014). Evidence from the genus *Pachycladon* suggests that gene flow may be relatively restricted across just a few hundred metres in elevation as species differentially adapt to local climatic conditions and soils (Joly *et al.*, 2014). Earlier-arriving genera also have a greater chance of becoming reproductively isolated by chromosomal rearrangement. If the probability of mutations increases with time (Meyers & Levin, 2006), earlier-arriving genera may produce more polyploid offspring, of which some can become new species. Some older genera, such as *Veronica*, do in fact contain several polyploid species, but others, such as *Anisotome*, have none, and young genera such as *Plantago* have many polyploids (Murray & de Lange, 2011). These patterns suggest that chromosomal rearrangement may be important but not a general mechanism of time-dependent diversification in the New Zealand flora. Hybridization may also have time-dependent outcomes for diversification. Invasion of new alpine habitats and environmental change, such as associated with glaciation cycles, may promote high degrees of hybridization (Saunders & Gibson, 2005). This has been shown to enhance the adaptive potential of earlier-arriving and hybridizing species (Becker *et al.*, 2013), and can lead to new species where hybrids exploit different habitats that are reproductively isolated from their parents (e.g. Rieseberg *et al.*, 2003). Later-arriving species hybridizing with resident taxa could also eventually disappear because of backcrossing (Herben *et al.*, 2005). Although these are all valid mechanisms explaining the greater diversity of earlier-arriving lineages, our plot-level analyses do implicate interspecific competition, resulting in niche preemption as an important process limiting levels of diversification (Silvertown, 2004).

Diversification interacts with emerging opportunity

We found that greater species diversity was correlated with greater access to niche space, and this was reduced by earlier-arriving taxa, suggesting that niche preemption may have

occurred despite environmental gradients expanding over time with mountain uplift (Fig. 2; Heenan & McGlone, 2013). Other explanations typically invoked for diversification slowdowns, such as a lack of geological and climatic events promoting allopatric speciation or geographic ranges that remain static and are increasingly divided by parapatry (Moen & Morlon, 2014), are thus unlikely because external factors have increased environmental space, potentially promoting speciation. One way in which early-arriving lineages might have filled more niche space to suppress diversification by later arrivals is if they could only establish on the low fertility of older soils below the treeline (Richardson *et al.*, 2004), because other habitats were unavailable, thereby enabling them to become superior competitors (Tilman, 1990). Several lineages that predate the formation of the Southern Alps do have origins in poorly drained and infertile sites, for example bogs (Heenan & McGlone, 2013), supporting the idea that they are more competitive. Earlier-arriving genera may also have colonized repeatedly, as they had more time to do so. If each colonization involved different ancestral genotypes, this could have enhanced levels of diversification and niche occupancy, although this possibility would still be consistent with our hypothesis of time-dependent access to niche space.

We also found evidence of time-dependent lineage diversification, independent of niche dynamics (Fig. 3). The simplest explanation for this result is that older lineages have had more time to accumulate differences that lead to speciation, such as by polyploidization or evolving traits that exploit environments in which populations become reproductively isolated. Thus, they can produce more species simply because they have survived longer irrespective of interlineage interactions. Linder (2008) speculated that this was possible in floras with limited extinction, whereby diversification rates did not vary with clade age. Future developments of our framework in Fig. 1 can incorporate these dynamics, as well as considering the potential for early colonizers to facilitate more niche space for later arrivals (e.g. Forbes *et al.*, 2009; Bailey *et al.*, 2013).

Of course, not all lineages diversify and our results show that lineage age is itself an important predictor of niche filling and subsequent community dominance (Fig. 3). One explanation for this is that earlier-arriving lineages may have had more time to accumulate phenotypic variation that fills niche space irrespective of the level of diversification (Paul *et al.*, 2009; He, 2013). For example, the snow tussock *Chionochloa* arrived c. 20 Mya and did not intensively diversify until the New Zealand alpine formed (Pirie *et al.*, 2010). The dominance of *Chionochloa* could therefore be a product of both its priority over niche space, which preempts later arrivals from communities, and its ability to diversify before later-arriving colonists, once new habitats emerged (Silvertown, 2004).

Preadaptation: finding the key with which to unlock opportunity

Our conceptual model suggests that colonizing species have traits that allow them to tolerate the abiotic conditions of their new

environments, thereby delaying extinction and/or increasing their susceptibility to speciation mechanisms (Simpson, 1944, 1953; Losos, 2010), but we did not find evidence for this with the traits that we studied. Ancestral habitat preference and life form only influenced community dynamics, not the extent of niche space that genera were able to diversify within (neutral effects in Fig. 3). One explanation is that these traits promote diversification non-linearly. Ancestors must be close enough in trait space to exploit new opportunities, but sufficiently distant so as not to be already highly adapted to their new environments (Knope *et al.*, 2012; see Fig. 1d). This is, in fact, predicted by mathematical theory underlying the search for adaptive peaks (Butler & King, 2004). Traits may evolve rapidly towards an optimum value, slowing down as they approach the optimum because selection weakens and drift becomes relatively large. In a landscape of multiple peaks, attraction will also depend upon distances to other optima and their selective strength, limiting the power of tests with single binary characters.

The evolution of physiological, morphological, and reproductive traits, for example associated with cold tolerance and edaphic preferences, is also likely to be correlated with shifts in diversification and speciation rates along evolutionary trees (Drummond *et al.*, 2012; Givnish *et al.*, 2014; Kostikova *et al.*, 2014; Litsios *et al.*, 2014). Traits that reduce extinction may also be important. For example, heterostyly in the Primulaceae does not drive speciation *per se* but reduces extinction by minimizing the negative effects of selfing (de Vos *et al.*, 2014). Improving the temporal resolution of correlations to identify traits that arise immediately before, as opposed to after, rate shifts is now needed to improve future predictions of when radiations arise and influence community assembly. Attempting to identify such functional traits has been routine in invasion biology, where the aim has been to predict traits that preadapt species to invade novel communities (Talentzap *et al.*, 2014).

Improving predictions of the ecological outcomes of plant radiations

What happens to radiations when a new lineage enters ecological communities depends on traits shaping their interspecific interactions (Fukami, 2015). Traits that enhance the competitiveness of lineages should promote diversification and niche filling (Simpson, 1953), and therefore complement the sequence in which lineages colonize sites. This has recently been found in the tropical forests of Amazonia, where highly diverse clades were associated with fast demographic traits that allowed them to dominate local vegetation plots (Baker *et al.*, 2014). Our study suggests that traits influencing time of arrival will also be important. Early-arriving immigrants are likely to have traits that allow them to colonize sites relatively quickly, such as long-distance dispersal, and then establish with positive growth and reproduction (McGill *et al.*, 2001; Waters *et al.*, 2013). Integrating data on such functional traits within a temporal context that predicts how they are used by species to access niche space should improve future predictions of when plant radiations influence community assembly and structure (Vannette & Fukami, 2014).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Predicted vs observed mean annual air temperature (MAT).

Fig. S2 Schematic of niche occupancy through time.

Table S1 Sources of lineage ages

Table S2 Sources of phylogeny data

Table S3 Model parameter estimates

Methods S1 Details of palaeoreconstructions.

Methods S2 Phylogeny estimation.

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