

Plant radiation history affects community assembly: evidence from the New Zealand alpine

William G. Lee^{1,2,*}, Andrew J. Tanentzap¹ and Peter B. Heenan³

¹Landcare Research, PB 1930, Dunedin 9054, New Zealand

²School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

³Landcare Research, PO Box 40, Lincoln 7640, Canterbury, New Zealand

*Author for correspondence (leew@landcareresearch.co.nz).

The hypothesis that early plant radiations on islands dampen diversification and reduce habitat occupancy of later radiations via niche pre-emption has never, to our knowledge, been tested. We investigated clade-level dynamics in plant radiations in the alpine zone, New Zealand. Our aim was to determine whether radiations from older colonizations influenced diversification and community dominance of species from later colonizations within a common bioclimatic zone over the past *ca* 10 Myr. We used stem ages derived from the phylogenies of 17 genera represented in alpine plant communities in the Murchison Mountains, Fiordland, and assessed their presence and cover in 262 (5 × 5 m) vegetation plots. Our results show clear age-related community assembly effects, whereby congeners from older colonizing genera co-occur more frequently and with greater cover per unit area than those from younger colonizing genera. However, we find no evidence of increased species richness with age of colonization in the alpine zone. The data support priority effects via niche pre-emption among plant radiations influencing community assembly.

Keywords: islands; plant radiations; community assembly; priority effects

1. INTRODUCTION

The order in which species enter a community, along with their relative competitive abilities, will determine their access to resources and may act as a major determinant of speciation rates among different radiations. Silvertown [1] noticed these ‘priority effects’ among radiations on islands, with older radiations producing seven times more endemic taxa than those derived from more recent radiations. He hypothesized that profuse speciation in a clade driven by strong intra-generic competition inhibited subsequent colonization by closely related taxa because of niche pre-emption from earlier arriving species capturing environmental space [2].

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2011.1210> or via <http://xxxx.royalsocietypublishing.org>.

Received 11 December 2011
Accepted 16 January 2012

The idea that priority effects among clades drive plant diversification via competitive exclusion has gained indirect support by the discovery that traits important for resource acquisition (within habitat, and related to differential resource consumption) often diverge early in plant radiations, whereas environmental niche traits (adaptations along macro-scale environmental gradients) appear regularly throughout radiations [3]. However, the suggestion that colonization timing and competition are key factors in the speciation of clades remains untested. Priority effects have been demonstrated experimentally to drive community assembly over ecological time [4], but their importance has rarely been tested in relation to macro-ecological patterns over evolutionary time-scales. Adaptive radiations in experimental microbial communities show that the sequence of immigration of different ancestral and specialist types into a spatially structured ecosystem has major impacts on diversification rates [5].

Here, we test the role of priority effects on speciation and community assembly using plant radiations in the New Zealand alpine zone as a model system. Vascular plant radiations contribute disproportionately to the New Zealand flora compared with many regions of the world, i.e. native genera with more than 20 species account for 42 per cent of vascular plant species. The majority of plant radiations are monophyletic, rapid and recent (< 10 Myr) [6], and the majority of species are widespread in non-forest habitats.

Time-calibrated molecular phylogenies are now available for most major lineages in the New Zealand alpine flora, thus allowing tests of the priority effect hypothesis. We compared species-rich genera, covering a range of growth forms and life-history features within representative alpine grasslands in southern South Island. Our objective was to test whether macro-evolutionary priority effects explained the composition of alpine plant communities, specifically, that competitive dominance by early-arriving clades reduced niche opportunities and diversification of later colonizing clades. We predicted that early-arriving (i.e. older) genera were more likely to co-occur with congeners, and dominate communities, than younger, late-arriving genera.

2. MATERIAL AND METHODS

(a) Study site

We investigated the alpine zone of the Murchison Mountains, New Zealand (780–1620 m above sea level; 45°15′S, 167°33′E), a 518 km² range of gneiss and granite with a narrow band of sedimentary rock along the eastern margin. A strong west-to-east rainfall gradient (*ca* 5000–2500 mm yr⁻¹) arises from the orientation of mountains across the path of prevailing winds. Vegetation above the treeline (*ca* 1100 m) is characterized by a band of low scrubland that makes a transition into snow tussock (*Chionochloa* spp.) grasslands, which dominate until replaced by alpine fellfield at *ca* 1430 m.

(b) Vegetation dataset

In 1980, we established 262 plots of 5 × 5 m, located above the treeline along 67 randomly positioned transects from valley floor to ridge top throughout the range. The percentage of ground area covered by each vascular plant species was visually estimated within each plot.

(c) Evolutionary ages of genera

We used molecular-based estimates of ‘stem’ ages (i.e. age for divergence from nearest relative outside New Zealand) for 17 focal monophyletic genera (hereafter termed focal genera) less than *ca* 10 Myr old (table 1), when the formation of upland ecosystems began in New Zealand [7]. We averaged values if two age estimates were available for a genus and propagated associated error estimates.

Table 1. Stem age, species richness and mean cover of 17 angiosperm genera in the Murchison Mountains, New Zealand. (Only the number of species in the Murchison Mountains and New Zealand are presented. Corresponding references in the electronic supplementary material.)

genera	stem age (variance)	no. spp. in Murchison Mountains	no. spp. in New Zealand	mean cover in plots (\pm s.e.)
<i>Abrotanella</i>	4.2 (0.44)	3	11	0.60 (0.21)
<i>Aciphylla</i>	8.4 (6.85)	8	37	0.98 (0.11)
<i>Anisotome</i>	11.1 (11.2)	5	17	1.52 (0.14)
<i>Chionochloa</i>	17.1 (3.09)	9	23	13.20 (0.76)
<i>Dracophyllum</i>	7.4 (3.76)	2	33	11.72 (1.13)
<i>Euphrasia</i>	5.7 (0.47)	4	16	0.20 (0.00)
<i>Forstera</i> / <i>Phyllachne</i>	6.3 (1.29)	2	8	1.19 (0.10)
<i>Gentianella</i>	2.1 (0.39) ^a	1	30	1.00 (0.00)
<i>Gingidia</i>	8.4 (6.76)	5	7	0.32 (0.03)
<i>Myosotis</i>	9.6 (9.57) ^a	1	38	0.20 (0.00)
<i>Oreobolus</i>	5.1 (0.81)	3	3	3.75 (0.67)
<i>Ourisia</i>	0.8 (0.07)	6	12	1.13 (0.10)
<i>Pachycladon</i>	1.6 (0.40)	1	10	0.20 (0.00)
<i>Plantago</i>	1.6 (0.16) ^a	1	10	1.91 (0.27)
<i>Ranunculus</i>	5.1 (0.73)	2	44	0.37 (0.04)
<i>Veronica</i>	9.7 (6.58)	12	124	4.24 (0.68)
<i>Wahlenbergia</i>	4.8 (2.14)	7	10	1.09 (0.14)

^aAverage of two estimates.

We tested whether older colonizations were more diverse. For each focal genus, we related its number of species (log-transformed) in our vegetation plots, and in all of New Zealand, to stem ages using Pearson's correlation tests.

(d) *Analyses of community dominance*

We tested whether species from older colonizations dominated the communities in which they occurred. For each of the vegetation plots, we summed the number of occurrences of individual species within the 17 focal genera. We then calculated the number of co-occurring species from any of 107 non-focal genera for each occurrence of a focal genus, and summed values across plots. We also summed the per cent cover of each focal genus across all plots along with the summed cover of co-occurring, non-focal genera.

We fitted linear models within a Bayesian framework to test the hypothesis that older genera were more likely to co-occur with congeneric species and with a greater per cent cover. For each focal genus, the log-transformed ratio of the number of congeneric species occurring per number of co-occurring species from non-focal genera, and the cover of a focal genus to cover of non-focal genera, were separately modelled as response variables. Stem age and the number of species in a focal genus that occurred in the Murchison Mountains were model predictors, each standardized to a mean of 0 and s.d. of 1. We accounted for the variance associated with estimates of stem age directly in our model and used Markov chain Monte Carlo sampling to estimate model parameters (see §3, electronic supplementary material for details). We inferred support for our hypotheses if 95% credible intervals (CIs) for the effects of stem age were positive and did not overlap zero.

3. RESULTS

Species richness, either within the alpine zone of the Murchison Mountains, or New Zealand, was unrelated to the age of the radiation ($r = 0.30$, $p = 0.258$ and $r = 0.35$, $p = 0.172$, respectively). Although more species-rich genera at both geographical scales were generally older than 5 Myr, there were also several species-poor genera among the older radiations, e.g. *Gingidia* (table 1; §2, electronic supplementary material).

Older radiations dominated the plots in which they occurred compared with more recently arrived genera. Both the number of co-occurring species of a focal

genus and their cover increased relative to their co-occurrence with non-congeneric genera as genera were increasingly older; 95% CIs for the effect of stem age: 0.04–0.28 and 0.25–1.53, respectively (figure 1). However, more diverse genera did not co-occur with congenics more frequently or with greater cover than with non-congeneric genera simply because of their greater diversity (95% CIs for effect of species number: –0.05 to 0.19 and –0.54 to 0.78, respectively). The number of occurrences of focal genera with congeneric species was overall much lower than with non-congenics (mean \pm s.e.: 1.13 ± 0.05 versus 25.1 ± 0.94 , respectively).

4. DISCUSSION

Few studies have compared the interactions and outcomes of interclade dynamics over evolutionary timescales within ecosystems where competition and environmental filtering influence community assembly. Our results from recent plant radiations in the alpine zone of New Zealand show that historical processes significantly impact the composition and structure of local plant communities [8]. Early radiations of shrub and herbaceous genera have more species and greater dominance across communities than later colonizations. The pattern of alpine community assembly has typically been interpreted on the basis of current environmental gradients, emphasizing temperature, soil nutrients, water and snow lie [9]. While these factors are important in structuring contemporary alpine communities, our results show that the arrival sequence and duration of genera in these communities also influences their composition.

Staggered arrival times of colonists throughout the Pliocene–Pleistocene, coupled with extreme climatic fluctuations, would have provided a labile and

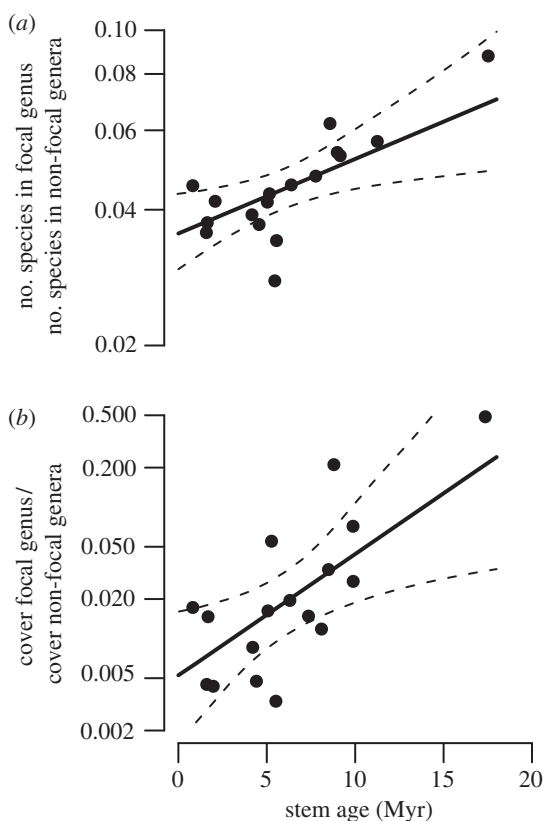


Figure 1. Relation between stem age, estimated after accounting for observation error (see §3, electronic supplementary material for explanation), and (a) relative number of congeneric species in focal/non-focal genera and (b) relative cover of congeneric species in focal/non-focal genera in 262 vegetation plots of 5 m², Murchison Mountains, Fiordland, New Zealand. The solid line is mean model fit \pm 95% CIs (electronic supplementary material, table S2). Bayesian $r^2 = 0.55$ and 0.44 for (a,b), respectively; $n = 17$.

compositionally different regional species pool at various times over the last 10 Myr, from which the alpine flora was derived. Chase [10] argues that historical contingency leading to potentially multiple stable equilibria is more likely in systems with a large regional species pool, low rates of dispersal, high productivity and low disturbance. However, few of these criteria apply to the alpine zone in New Zealand [9], suggesting that a historically variable and periodically augmented species pool may have a range of assembly drivers, while retaining a strong historically determined structure.

Silvertown *et al.* [1] emphasized the importance of niche pre-emption as the mechanism driving both community dominance and speciation, especially during early phases of an evolutionary radiation. Evidence from our study for strong competitive effects can be inferred from the: (i) relative dominance of early radiations, and (ii) greater number of congenics coexisting at the vegetation plot scale. Silvertown *et al.* [1,2] perceived adaptive radiations to be driven by strong congeneric competition within the same habitat, at least initially, until species became segregated along environmental gradients. One potential mechanism for niche pre-emption on islands is insular

gigantism [11], whereby plants increase in height with time since colonization. In our study, older herbaceous genera, for example *Anisotome*, are noticeably taller than recent arrivals (e.g. *Pachycladon*), which would improve access to resources and is an evolutionary advantage in most habitats [12].

The pattern of lineage diversification in the alpine zone of New Zealand is emerging from molecular studies of the major genera. Repeated cycles of range expansion and contraction during the Pleistocene, hybridization and recolonization by montane species [13] have all promoted speciation in alpine habitats. However, within the time window we studied, i.e. ca the last 10 Myr, there was no evidence that colonization history influences diversification across the New Zealand alpine. Species richness was greater in older genera but species-poor genera of similar age were equally common at both. Current species pools are the net outcome of immigration, speciation and extinction processes, potentially confounding generalizations associated with colonization age and diversification, especially during periods of climate extremes and geographical range adjustments.

The effects of colonization sequence in the origin of New Zealand vegetation have been largely overlooked, although there is now considerable evidence for the importance of immigration in the composition of the flora. Our results provide, to our knowledge, the first evidence for the importance of colonization history in the composition and structure of contemporary communities within a major adaptive zone. This supports the growing number of examples demonstrating that contingency is of widespread importance in the evolution of biodiversity and ecosystem processes.

We thank two reviewers for improvements to the manuscript, David Bryant for advice with statistical analyses and authors of several phylogenies used for assistance in determining error estimates around divergence times.

- 1 Silvertown, J. 2004 The ghost of competition past in the phylogeny of island endemic plants. *J. Ecol.* **92**, 168–173. (doi:10.1111/j.1365-2745.2004.00853.x)
- 2 Silvertown, J., Francisco-Ortega, J. & Carine, M. 2005 The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations. *J. Ecol.* **93**, 653–657. (doi:10.1111/j.1365-2745.2005.01038.x)
- 3 Ackerly, D. D., Schwillk, D. E. & Webb, C. O. 2006 Niche evolution and adaptive radiation: testing the order of trait divergence. *Ecology* **87**, S50–S61. (doi:10.1890/0012-9658(2006)87[50:NEAART]2.0.CO;2)
- 4 Fukami, T. 2004 Assembly history interacts with ecosystem size to influence species diversity. *Ecology* **85**, 3234–3242. (doi:10.1890/04-0340)
- 5 Fukami, T., Beaumont, H. J. E., Zhang, X.-X. & Rainey, P. B. 2007 Immigration history controls diversification in experimental adaptive radiation. *Nature* **446**, 436–439. (doi:10.1038/nature05629)
- 6 Linder, H.P. 2008 Plant species radiations: where, when, why? *Phil. Trans. R. Soc. B* **363**, 3097–3105. (doi:10.1098/rstb.2008.0075)
- 7 Lee, D. E., Lee, W. G. & Mortimer, N. 2001 Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to

- palaeogeography and climate. *Aust. J. Bot.* **49**, 341–356. (doi:10.1071/BT00031)
- 8 Herrera, C. M. 1992 Historical effects and sorting processes as explanations of contemporary ecological patterns: character syndromes in Mediterranean woody plants. *Am. Nat.* **140**, 421–446. (doi:10.1086/285420)
- 9 Wardle, P. 1991 *Vegetation of New Zealand*. Cambridge, UK: Cambridge University Press.
- 10 Chase, J. M. 2003 Community assembly: when should history matter? *Oecologia* **136**, 489–498. (doi:10.1007/s00442-003-1311-7)
- 11 Palkovacs, E. P. 2003 Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* **103**, 37–44. (doi:10.1034/j.1600-0706.2003.12502.x)
- 12 Falster, D. S. & Westoby, M. 2003 Plant height and evolutionary games. *Trends Ecol. Evol.* **18**, 337–343. (doi:10.1016/S0169-5347(03)00061-2)
- 13 Winkworth, R. C., Wagstaff, S. J., Glenny, D. & Lockhart, P. J. 2005 Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organisms Divers. Evol.* **5**, 237–247. (doi:10.1016/j.ode.2004.12.001)