

# Evolutionary priority effects in New Zealand alpine plants across environmental gradients

Devin R. Leopold<sup>1\*</sup>, Andrew J. Tanentzap<sup>2</sup>, William G. Lee<sup>3,4</sup>, Peter B. Heenan<sup>5</sup> and Tadashi Fukami<sup>1</sup>

<sup>1</sup>Department of Biology, Stanford University, Stanford, California, USA, <sup>2</sup>University of Cambridge, Cambridge, UK, <sup>3</sup>Landcare Research, Dunedin, New Zealand, <sup>4</sup>School of Biological Sciences, University of Auckland, Auckland, New Zealand, <sup>5</sup>Landcare Research, Canterbury, New Zealand

## ABSTRACT

**Aim** Priority effects, in which the order and timing of species arrival influence community assembly, are thought to be stronger in less stressful environments, reflecting increased competition, but this hypothesis has rarely been examined over evolutionary time. Here, we test the hypothesis using an island community of alpine plants.

**Location** Murchison Mountains, South Island, New Zealand.

**Methods** Lineage age data for 14 monophyletic New Zealand alpine plant genera, with stem ages ranging from 2 to 17 Ma, were paired with species presence and abundance data in 261 plots, covering nearly 400 km<sup>2</sup>. The relationships between lineage age and the relative abundance and richness of focal genera across elevation (800–1620 m) and precipitation (2500–5000 mm yr<sup>-1</sup>) gradients were investigated using linear models in a Bayesian framework.

**Results** The relative abundance of focal genera increased with lineage age, but this effect was weaker at higher elevation and precipitation, where plants are likely to have experienced more stressful conditions. The relative richness of focal genera increased at a consistent rate despite significant changes in overall richness of focal genera across both elevation and precipitation gradients.

**Main conclusions** Our results suggest that priority effects, on a time-scale of millions of years and involving significant evolutionary change, influence community assembly, leading to increased dominance of older lineages, but that the strength of these effects may vary with environmental conditions. Environmental gradients correlated with abiotic stress, such as elevation in alpine systems, may be particularly important for predicting the strength of both ecological and evolutionary priority effects.

## Keywords

Abiotic stress, colonization, community assembly, dispersal, historical contingency, immigration history, island diversification, New Zealand, niche pre-emption, stress gradient hypothesis.

\*Correspondence: Devin R. Leopold, Stanford University, Department of Biology, Stanford, CA 94305-5020, USA.  
E-mail: devin.leopold@gmail.com

## INTRODUCTION

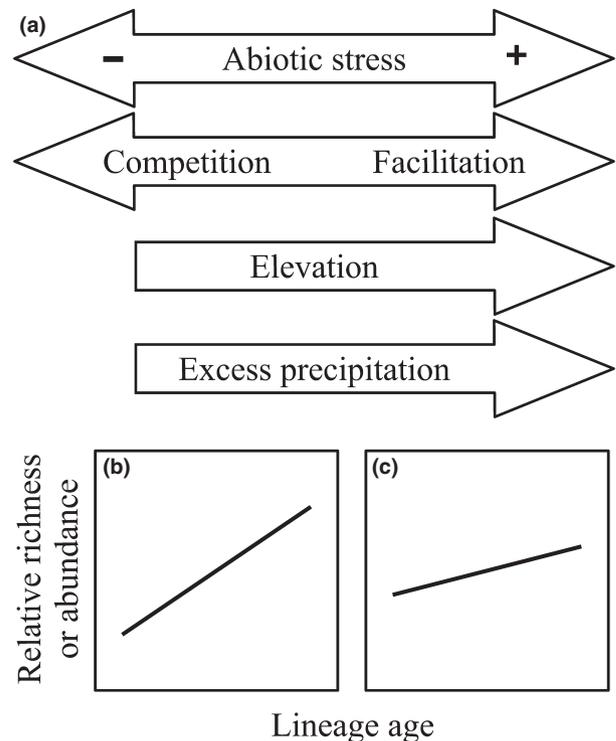
It is now well recognized that the order and timing of species arrival can influence the trajectory of community assembly and the resulting patterns of species abundance and distribution, a phenomenon known as priority effects (e.g. Drake, 1991; Fukami, 2004; Urban & De Meester, 2009; Geange & Stier, 2010). Priority effects present a fundamental challenge in explaining species abundance and distribution because species arrival history is often impossible to know in

sufficient detail (Fukami, 2015). An increasing number of studies suggest, however, that the strength of priority effects can be predicted from environmental conditions (e.g. Chase, 2003, 2007; Donohue *et al.*, 2009). Underlying some of these studies is the well-established stress gradient hypothesis (SGH), which posits that increasing abiotic stress limits resource acquisition and biomass accumulation, reducing the competition between neighbouring plants and providing greater opportunity for facilitative interactions (Bertness & Callaway, 1994; Brooker & Callaghan, 1998; Callaway *et al.*,

2002). If the SGH is true, then in cases where priority effects influence community assembly primarily through competition (Belyea & Lancaster, 1999), the strength of priority effects should diminish with increased abiotic stress.

Although the prediction that priority effects are weaker under more stressful conditions has received some experimental support over ecological time (e.g. Chase, 2007; Kardol *et al.*, 2013; Vannette & Fukami, 2014), it has rarely been tested over evolutionary time despite the potential for priority effects to influence communities over a range of time-scales. Clearly, a main reason for the lack of relevant work is the difficulty in conducting manipulative experiments over the many generations required (but see Fukami *et al.*, 2007; Knope *et al.*, 2012). Nonetheless, the relationship between community structure and estimated arrival time of ancestral species can provide insight into evolutionary processes that cannot be observed directly or evaluated experimentally (e.g. Losos *et al.*, 1998; Gillespie, 2004; Silvertown, 2004; Swenson, 2011; Patiño *et al.*, 2013; Richardson *et al.*, 2014). Modern advances in phylogenetic analysis (Cavender-Bares *et al.*, 2009) and molecular dating (Kumar, 2005) now provide the tools necessary to reconstruct, with increasing confidence, the order of successful species arrival over evolutionary time and to investigate evolutionary priority effects (Gehrke & Linder, 2011; Cornuault *et al.*, 2013). This is particularly true in isolated island systems, where endemism and monophyly are more common than in continental systems (Schluter, 2000). Most recently, a study of monophyletic plant radiations in the New Zealand alpine zone demonstrated that the timing of arrival to New Zealand was negatively correlated with measures of community dominance at the landscape scale, indicating evolutionary priority effects (Lee *et al.*, 2012). However, that study did not address how spatial variation in environmental conditions may affect the strength of priority effects.

In this paper, we investigate how lineage age and environmental conditions interactively influence local community patterns, by expanding the analysis presented in Lee *et al.* (2012). Unlike Lee *et al.* (2012), who analysed plant abundance data summed across an entire region, this study focuses on smaller-scale abundance data at the level of individual 25-m<sup>2</sup> plots. This allows us to ask whether priority effects vary in strength across environmental gradients, specifically elevation and precipitation. Elevation was used as a proxy for temperature and abiotic stress (Choler *et al.*, 2001), and precipitation for decreased nutrient availability and ecosystem productivity, from mesic to wet, due to soil saturation and anoxia (Schoor & Matson, 2001). Applying the SGH, we hypothesized that the strength of evolutionary priority effects would attenuate with increased abiotic stress. Because we expected abiotic stress to increase with elevation and precipitation (Fig. 1a), we hypothesized that the effect of lineage age on relative abundance and richness would decrease across these environmental gradients (Fig. 1b,c). We chose to use the alpine zone for this study because the steep temperature gradient provides an ideal, and widely used,



**Figure 1** Schematic depiction of the hypothesis we tested regarding how the strength of evolutionary priority effects varies with environmental gradients such as elevation and precipitation. (a) This hypothesis is built on the stress gradient hypothesis, which predicts that increasing abiotic stress results in a shift from competitive to facilitative interactions. Increasing elevation and excess precipitation ( $> 2500 \text{ mm yr}^{-1}$ ) are used here as natural gradients of increasing abiotic stress and are hypothesized to correlate with decreasing competitive interactions. (b) Relative abundance or richness of a lineage (i.e. genus) is hypothesized to increase in magnitude with lineage age, indicating evolutionary priority effects. (c) However, here we further hypothesize that increasing abiotic stress weakens evolutionary priority effects, which would result in a shallower slope in the relationship between relative abundance or richness and lineage age.

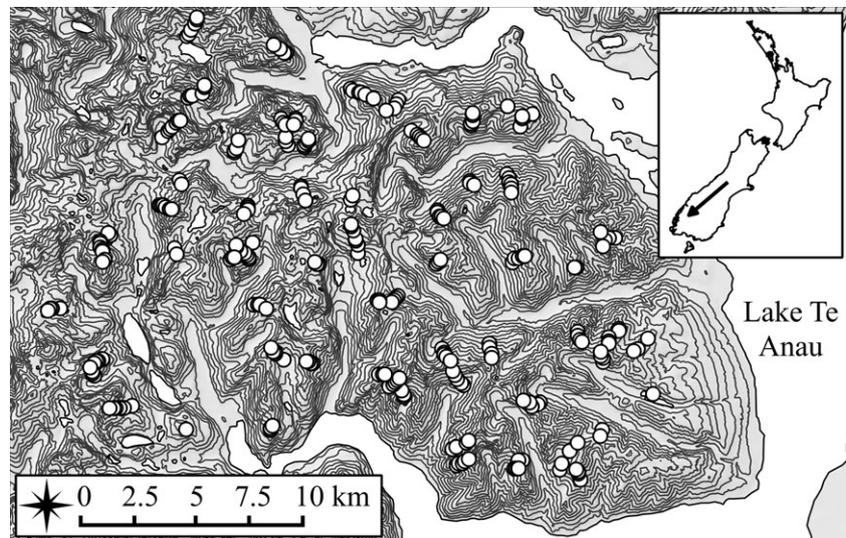
model system for testing SGH-based hypotheses (Choler *et al.*, 2001; Callaway *et al.*, 2002; Butterfield *et al.*, 2013).

## MATERIALS AND METHODS

### Data

Vegetation data were collected in 1980 and 1981 in the alpine zone of the Murchison Mountains, New Zealand (Fig. 2). Terrain at the study site consists of alternating ridges and valleys 780–1620 m above sea level, with a mean temperature decrease of 1 °C per 100 m of elevation gain (Tanentzap *et al.*, 2012). Plots (5 m × 5 m) were placed at intervals  $> 100 \text{ m}$  along 67 randomly placed transects, spanning the tree line to the ridge top and distributed over approximately 400 km<sup>2</sup>, with an underlying east to west

**Figure 2** Shaded relief and 250-m contour map of the study site in the Murchison Mountains on New Zealand's South Island. The map inset indicates the study location in New Zealand. Plant data were collected in 261 plots (open circles) above the tree line at elevations of 780–1620 m a.s.l. Precipitation increases from mesic to wet (approximately 2500–5000 mm yr<sup>-1</sup>) from east to west. Map layers were sourced from the LINZ Data Service (<http://data.linz.govt.nz/>) and licensed for use by LINZ under the Creative Commons Attribution 3.0 New Zealand licence.



precipitation gradient, from mesic to wet (c. 2500–5000 mm yr<sup>-1</sup>). Across 261 plots, 278 vascular plant species were identified and total percentage cover for each species was visually estimated, allowing for > 100% cover in plots where vegetation overlapped in height and < 100% when bare ground or rock was present.

Following Lee *et al.* (2012), we focused our analysis on monophyletic genera with well-documented phylogenies and published divergence time estimates. Immigration timing cannot be known exactly, and estimates of the age of ancestral nodes on time-calibrated phylogenies provide the best available estimate of lineage age. We included the additional constraint that species from each focal genus be present in a minimum of four plots, resulting in a mean of 115 (range: 4–252) observations per genus. This resulted in 14 monophyletic genera with stem ages (age of the most recent common ancestor shared by the New Zealand clade and its nearest extant relative) ranging from 1.6 to 17.1 Ma (Table 1). Insufficient published data precluded the use of crown age (age of the most recent common ancestor of the New Zealand clade) in this analysis, but crown age did correlate with stem age in the nine genera for which data were available ( $r = 0.76$ ;  $P = 0.019$ ). Estimates of stem age and associated uncertainty were compiled and standardized from published sources, which used a variety of gene regions and molecular-clock methods to estimate divergence times (see Lee *et al.*, 2012, and references therein for details). For sources reporting 95% highest posterior densities, the uncertainty of stem age estimates were standardized by estimating a variance using the longer of the two tails and assuming a normal distribution around the mean.

### Statistical analysis

We used relative generic abundance and relative generic richness as measures of community dominance. We defined

relative generic abundance as the percentage cover of a focal genus divided by the percentage cover of all other species and relative generic richness as the number of species of a focal genus divided by the number of all other species, as in Lee *et al.* (2012). Both measures of community dominance were calculated in each plot for all focal genera present, resulting in 1611 unique observations across 261 plots.

We used linear models to test the hypothesis that relative generic abundance and richness increased with stem age, but that this effect was weaker at higher elevation and precipitation. We assumed that the estimated dominance (either abundance or richness),  $c_{ij}$ , of genus  $i$  in plot  $j$  was derived from a log-normal distribution and could be modelled as:

**Table 1** Focal genera of New Zealand alpine plants used in this study and compiled, published mean estimated age of the most recent ancestor prior to arrival in New Zealand (stem age, Ma) and standardized variance measures (for sources, see Lee *et al.*, 2012, and references therein). All species in our data are native to New Zealand.

Genus	Family	Growth form	Stem age (variance) (Ma)
<i>Abrotanella</i>	Compositae	Cushion	4.20 (0.66)
<i>Aciphylla</i>	Umbelliferae	Herb	8.36 (2.62)
<i>Anisotome</i>	Umbelliferae	Herb	11.05 (3.35)
<i>Chionochloa</i>	Gramineae	Graminoid	17.05 (1.76)
<i>Dracophyllum</i>	Ericaceae	Cushion/shrub	7.40 (1.94)
<i>Euphrasia</i>	Orobanchaceae	Herb	5.70 (0.69)
<i>Forstera</i>	Stylidiaceae	Herb	6.32 (1.14)
<i>Gentianella</i>	Gentianaceae	Herb	2.05 (0.63)
<i>Hebe</i>	Plantaginaceae	Herb	9.69 (2.56)
<i>Oreobolus</i>	Cyperaceae	Graminoid	5.10 (0.90)
<i>Pachycladon</i>	Cruciferae	Herb	1.61 (0.63)
<i>Plantago</i>	Plantaginaceae	Herb	1.62 (0.40)
<i>Ranunculus</i>	Ranunculaceae	Herb	5.05 (0.85)
<i>Wahlenbergia</i>	Campanulaceae	Herb	4.80 (1.47)

Model 1:

$$c_{ij} \sim \ln N(\mu_{ij}, \sigma^2)$$

$$\mu_{ij} = \alpha + \beta_1(\text{Stem}_i) + \beta_2(\text{Alt}_j) + \beta_3(\text{East}_j) \\ + \beta_4(\text{Stem}_i \times \text{Alt}_j) + \beta_5(\text{Stem}_i \times \text{East}_j) + \text{Plot}_j \\ + \text{Genus}_i,$$

where log-transformed mean dominance values ( $\mu_{ij}$ ) were modelled as a response of the stem age of genus  $i$  ( $\text{Stem}_i$ ), and elevation ( $\text{Alt}_j$ ) and easting ( $\text{East}_j$ ) of plot  $j$ . Easting was used as a proxy for precipitation; greater values correspond to decreasing precipitation. We also accounted for random variation in  $\text{Plot}$  and  $\text{Genus}$ . Owing to significant heteroscedasticity in the relative abundance data, a variance structure was implemented by estimating a unique variance ( $\sigma^2_i$ ) for each genus  $i$ . The variance structure did not improve the model fit for relative richness, so we present results from the simpler model.

All statistical analyses were conducted in the R 3.0.2 environment (R Core Team, 2013). The model was fitted in a Bayesian framework in the RSTAN 2.2.0 package (Stan Development Team, 2014). Because uncertainties associated with estimates of phylogenetic divergence are highly variable, errors associated with published stem-age estimates were propagated forward through the analysis using a Bayesian errors-in-variables model (Richardson & Gilks, 1993). Thus, an advantage of using a Bayesian framework like ours is that it allows us to take into account differences in the degree of error associated with compiled stem-age estimates by repeatedly sampling from a distribution of possible stem-age values for each focal genus. Briefly, the true stem ages,  $\text{Stem}_i$ , in Model 1 were treated as unknown values with informative priors, where the published mean ( $s_i$ ) and variance ( $\varepsilon_i$ ) for each genus  $i$  were used to define a distribution of possible stem-age values [ $\text{Stem}_i \sim N(s_i, \varepsilon_i)$ ], which was sampled randomly at each model iteration.

All estimated model parameters were assigned non-informative priors, and all predictor variables were scaled to a mean of 0 and a standard deviation of 1 so that their effects were directly comparable. Posterior distributions of model parameters were estimated from 1000 samples from each of three independent Markov chains. Convergence of the three independent chains and sufficient sampling of posterior distributions were confirmed by visual inspection of parameter traces, ensuring a scale reduction factor below 1.01, and an effective sample size of at least 1000 (Gelman & Hill, 2007). Model parameters were considered significant when the 95% credible intervals (CIs) of their posterior distributions excluded zero. Therefore, support for the hypothesis that priority effects were weaker under greater abiotic stress could be drawn from a significant positive coefficient for the interaction between stem age and elevation and a negative coefficient for the interaction between stem age and easting.

A posterior predictive check (PPC) was used to assess the overall model fit (Gelman & Hill, 2007; Kéry, 2010). Briefly,

at each iteration, a synthetic data set was drawn from the modelled distribution, and the sums of standardized squared residuals of this simulated ‘ideal’ data were calculated. The PPC is presented as the proportion of model iterations where the sums of squared model residuals from the actual data are greater than from the simulated data, resulting in values close to 0.5 for models that are well matched to the data. Additionally, a Bayesian  $R^2$  statistic was calculated as 1 minus the ratio of the average posterior residual variance divided by the variance in the raw data, which is interpreted identically to the classical  $R^2$  (Gelman & Pardoe, 2006).

To evaluate potential alternative explanations of our results, not related to priority effects *per se*, we tested three alternative models, each with an additional parameter. First, we tested for the possibility that our results could be explained by variation in relative richness among focal genera by including the total richness for each genus as a model predictor. Second, because total vegetative cover decreased with elevation and easting (elevation,  $r = -0.31$ ,  $P < 0.001$ ; easting,  $r = -0.21$ ,  $P < 0.001$ ), we tested whether the observed variation in community dominance measures was simply due to a change in total vegetative cover by including total cover in each plot as a predictor. Third, we checked for the sensitivity of the results to the removal of *Chionochloa*, by far the oldest (17.1 Ma) and most dominant lineage in the dataset (mean cover  $\pm$  SD = 25.8%  $\pm$  21.0%).

## RESULTS

We confirmed that the increased dominance of older lineages at the landscape level reported by Lee *et al.* (2012) arose at the plot scale (Table 2). Both relative abundance and relative

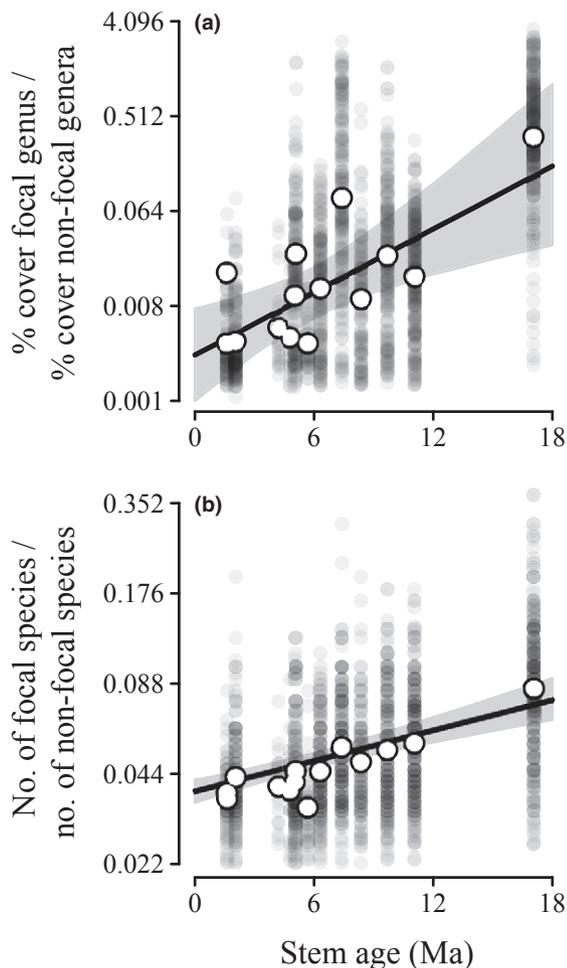
**Table 2** Means and 95% credible intervals of model parameters for both relative generic abundance (cover of a focal genus/cover of non-focal genera) and relative generic richness (no. of species from a focal genus/no. of species from other genera) for alpine plants in New Zealand.

Parameters	Relative abundance			Relative richness		
	Mean	95% credible interval		Mean	95% credible interval	
Intercept	<b>-4.39</b>	<b>-4.91</b>	<b>-3.86</b>	<b>-3.01</b>	<b>-3.06</b>	<b>-2.96</b>
Stem age	<b>1.05</b>	<b>0.43</b>	<b>1.59</b>	<b>0.17</b>	<b>0.13</b>	<b>0.21</b>
Elevation	<b>0.17</b>	<b>0.10</b>	<b>0.24</b>	<b>0.04</b>	<b>0.01</b>	<b>0.07</b>
Easting	-0.05	-0.12	0.02	<b>0.16</b>	<b>0.12</b>	<b>0.19</b>
Stem age $\times$ elevation	<b>-0.12</b>	<b>-0.19</b>	<b>-0.06</b>	0.00	-0.01	0.02
Stem age $\times$ easting	<b>0.06</b>	<b>0.01</b>	<b>0.12</b>	-0.01	-0.02	0.01
Genus	<b>0.91</b>	<b>0.47</b>	<b>1.53</b>	<b>0.05</b>	<b>0.01</b>	<b>0.12</b>
Plot	<b>0.35</b>	<b>0.27</b>	<b>0.43</b>	<b>0.25</b>	<b>0.22</b>	<b>0.28</b>

Bold values indicate cases where credible intervals do not include zero. Values for Plot and Genus are posterior distributions of the standard deviation of the random effects.

richness increased with stem age, with the former having a stronger effect [95% CIs: (0.43, 1.59) and (0.13, 0.21), respectively; Fig. 3].

We also found that the effect of stem age on relative abundance was significantly reduced with elevation and precipitation (lower easting), although the effect size of the latter was smaller [95% CIs: (−0.19, −0.06) and (0.01, 0.12), respectively; Fig. 4a,b]. In contrast, the effect of stem age on relative richness did not vary significantly with elevation or precipitation [95% CIs: (−0.01, 0.02) and (−0.02, 0.01), respectively; Fig. 4c,d], and relative richness overall increased with elevation and decreased with precipitation [95% CIs: (0.01, 0.07) and (0.12, 0.19), respectively]. Relative abundance similarly increased with elevation but did not change with precipitation [95% CIs: (0.10, 0.24) and (−0.12, 0.02), respectively].



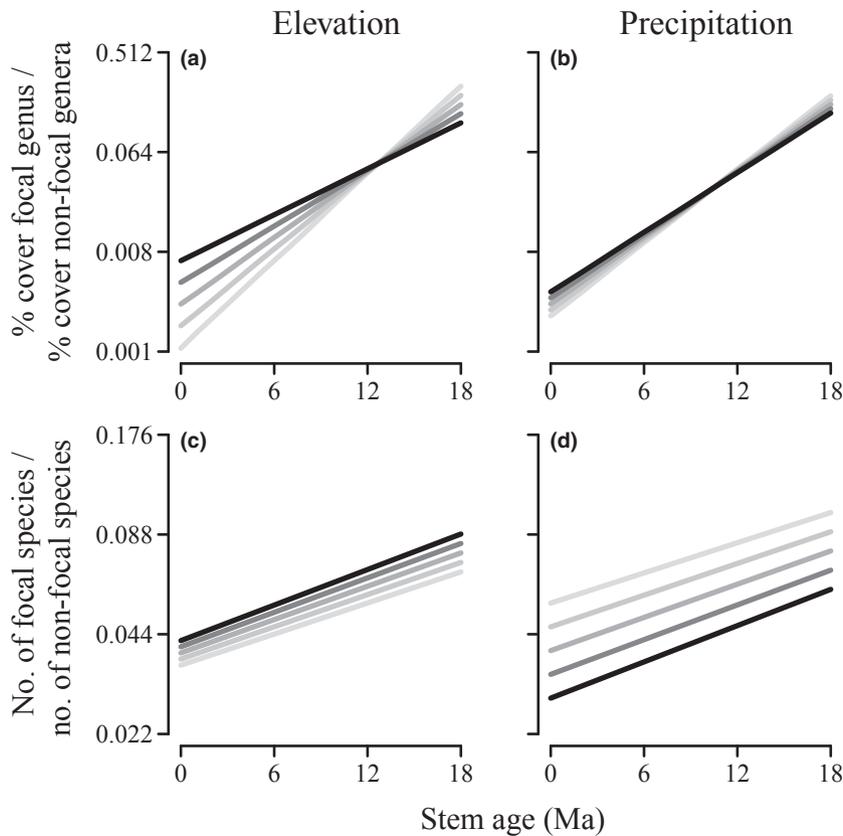
**Figure 3** Model results for the mean relationship between stem age and (a) relative abundance and (b) relative richness of alpine plants in New Zealand, with 95% credible intervals indicated by grey polygons (Bayes  $R^2 = 0.56$  and  $0.57$ , respectively;  $y$ -axes are on logarithmic scales). Larger white circles indicate mean values for each focal genus ( $n = 14$ ). Semitransparent grey circles are individual observations ( $n = 1611$ ).

Overall, the posterior predictive check indicated that the distribution of the data generally matched the modelled distributions (relative abundance, PPC 0.43; relative richness, PPC 0.49), and both models explained a substantial portion of the variance in the data (Bayes  $R^2$  of 0.56 and 0.57, respectively).

None of the three alternative hypotheses explained our results as well as the priority effects hypothesis did (see Appendix S1 in Supporting Information). First, neither relative abundance nor richness varied significantly with total richness of focal genera [95% CIs: (−0.27, 0.28) and (−0.01, 0.03), respectively; Appendix S1a]. Including the richness of focal genera as a predictor did cause the posterior distribution of the interaction between stem age and easting to cross zero for the relative abundance model [95% CI: (−0.01, 0.12)], highlighting the marginal support for this parameter as a predictor. Second, including the total vegetative cover of each plot did not significantly change the effect of elevation or precipitation on the relationship between stem age and relative abundance or cover. Relative abundance and richness did decrease significantly with total cover [95% CIs: (−0.43, −0.30) and (−0.08, −0.01); Appendix S1b], and the inclusion of total cover in the model reduced support for the effect of elevation [95% CIs: (−0.04, 0.08) and (−0.02, 0.06), for relative abundance and richness, respectively], due to correlation between the posterior parameter estimates for elevation and cover ( $r = 0.40$  &  $0.36$ , respectively;  $P < 0.001$  in both cases). Finally, although the exclusion of *Chionochoa* changed the mean estimates of some model parameters (Appendix S1c), the significance of the effects of elevation and precipitation on the relationship between stem age and relative abundance and cover remained.

## DISCUSSION

Our results should be interpreted within the context of the dynamic environmental changes that occurred as our focal plant lineages arrived and diversified. In New Zealand, geological upheaval, initiating the formation of cool, open habitats, began as early as 5 Ma (Batt *et al.*, 2000) and intermittent glaciation throughout the Pliocene and Pleistocene is thought to have resulted in a cyclical pattern of formation and destruction of precursor alpine habitat (Wardle, 1963). Analogues of contemporary alpine habitats were not consistently present until about 1.2 Ma (Heenan & McGlone, 2013), well after our youngest focal lineages are thought to have arrived. These geological changes and environmental fluctuations may have caused the repeated expansion and contraction of species ranges, limiting opportunities for the formation of monophyletic groups of alpine specialists, while providing opportunities for established lineages to diversify and expand their distributions (McGlone *et al.*, 2001; Winkworth *et al.*, 2005; Linder, 2008). Our results on relative abundance and relative richness are therefore both an outcome of this environmental context.



**Figure 4** Predicted relationship between stem age and relative abundance of alpine plants in New Zealand with (a) elevation and (b) precipitation, and the predicted relationship between stem age and relative richness with (c) elevation and (d) precipitation (*y*-axes are on logarithmic scales). Relationships are estimated for five equally spaced intervals of elevation and precipitation, increasing from light grey to black, across the range found in the data set (780–1620 m a.s.l. and 2500–5000 mm yr<sup>-1</sup>, respectively). See Table 2 for statistical details.

### Relative abundance

Consistent with our hypothesis, we found that the greater relative abundance of older lineages diminished with increased elevation and, to a lesser degree, increased precipitation (Fig. 4a). Given previous reports of a decreasing role of competition with elevation in alpine plants (Callaway *et al.*, 2002), this result supports the hypothesis that evolutionary priority effects are at least partly driven by competitive interactions. If elevation in alpine systems was a proxy for abiotic stress, and if SGH predictions were broadly applicable, results from elevation gradients should be supported by those from other environmental stress gradients. Here, we found that precipitation was an additional gradient that supported the idea of competitive interactions influencing evolutionary priority effects, in that the increase in relative abundance with stem age was reduced with increasing precipitation (Fig. 4b). That this effect was weaker than the effect of elevation may be because easting – our proxy for precipitation – did not capture relevant variation at smaller scales, such as with aspect, or because the range of precipitation represented a narrower range of abiotic stress than was captured by elevation.

The increased relative abundance of older lineages may be because they have had more time to adapt to the environmental conditions above the tree line. This idea is, however, inconsistent with the timing of alpine habitat formation. Because contemporary alpine habitats did not begin to form

until at least 2 Ma (Heenan & McGlone, 2013), most lineages in our study would have had an equivalent amount of time to expand into the alpine habitat as it was forming.

There are at least three potential mechanisms that may explain how early immigration prior to the formation of contemporary alpine habitats resulted in high relative abundance of the older lineages. First, adaptation to cool climates in precursor alpine habitat by early-arriving lineages may have facilitated a subsequent rapid colonization of modern alpine habitat. Consistent with this idea, in many older lineages, alpine-inhabiting congeners are more closely related to disparate generalist and lowland species than to one another (Lockhart *et al.*, 2001; Pirie *et al.*, 2010). Second, range overlap among closely related species may have facilitated rapid adaptation and the colonization of novel habitats through hybridization (Becker *et al.*, 2013). Hybridization may also have allowed species adapted to cool climates to persist when these habitats were periodically absent. Third, older lineages may have been more widespread in non-alpine habitats and had therefore had more opportunity to colonize new alpine habitat in greater numbers, potentially limiting the expansion and diversification of younger lineages (Price *et al.*, 2014). Whatever the actual mechanisms of priority effects may have been, what is intriguing about our results is that the strength of the mechanisms varied along elevation and precipitation gradients.

We cannot completely discard the hypothesis that patterns of increasing relative abundance with lineage age are simply

a result of older lineages having had a longer time for population growth, without interspecific competition playing any major role. However, given the time-scale involved, most if not all lineages seem likely to have had ample time to approach their carrying capacity in the alpine zone. Furthermore, a simple explanation based on population growth seems unable to address why the strength of the lineage age effect on relative abundance should vary with elevation and precipitation.

### Relative richness

In contrast to relative abundance, we found no strong support for an effect of elevation or precipitation on the relationship between stem age and relative richness (Fig. 4c,d), suggesting that it may be more difficult for older lineages to exclude entire species than it is to reduce their abundance. This may be expected because abundance can change without a corresponding change in species identity. It is also possible that plant traits that influenced relative abundance (e.g. relative growth rate or specific leaf area) were under selection by elevation and precipitation, whereas those that influenced relative richness (e.g. reproductive isolation or niche differentiation) were not.

Immigration timing is often a strong predictor of clade richness (Gehrke & Linder, 2011; Cornuault *et al.*, 2013), with early-arriving lineages diversifying more. It may be argued that the greater relative richness of older lineages at the plot scale may simply be due to the increased time over which adaptive radiation occurred, rather than indicating anything about priority effects, but this possibility is not supported by our alternative models, which failed to detect the total species richness of focal genera as a significant predictor for either measure of community dominance. Furthermore, Lee *et al.* (2012) reported that, although older lineages at this site appeared to be more species-rich, the correlation was not statistically significant. Older lineages may have also experienced greater numbers of extinctions, obscuring the effect of stem age on the richness of older radiations and limiting our ability to discount a 'time-to-diversify' mechanism. The inclusion of clade richness reduced support for the interaction between stem age and precipitation, although the effect size remained unchanged, suggesting that clade richness may be important. Nonetheless, the lack of a significant direct effect of clade richness, along with the consistent effect of stem age on relative richness and abundance at the plot scale, suggests that older lineages tend to co-occur and codominate to a greater degree than younger lineages for reasons other than richness alone.

### CONCLUSIONS

As suggested previously (e.g. Silvertown, 2004; Herben *et al.*, 2005; Silvertown *et al.*, 2005; Lee *et al.*, 2012) and corroborated here, the abundance and distribution of species can be greatly influenced by immigration history over millions of

years. These evolutionary priority effects make patterns of abundance and distribution difficult to understand, but we have demonstrated here that the strength of these effects may be systematically predictable along environmental gradients. As more accurate molecular estimates of immigration history become available, it should be possible to apply the approach taken here to other taxa and locations, thereby improving the general understanding of community assembly and biogeography.

### ACKNOWLEDGEMENTS

We thank Angela Brandt and the members of the community ecology group at Stanford University, particularly Rachel Vannette, for comments. James Richardson, Robert J. Whitaker, and three anonymous referees helped to improve the clarity of the manuscript. We also thank the Department of Conservation, New Zealand, for access to the vegetation data and the Royal Society of New Zealand Marsden Fund for funding.

### REFERENCES

- Batt, G.E., Braun, J., Kohn, B.P. & McDougall, I. (2000) Thermochronological analysis of the dynamics of the Southern Alps, New Zealand. *Geological Society of America Bulletin*, **112**, 250–266.
- Becker, M., Gruenheit, N., Steel, M., Voelckel, C., Deusch, O., Heenan, P.B., McLenachan, P.A., Kardailsky, O., Leigh, J.W. & Lockhart, P.J. (2013) Hybridization may facilitate *in situ* survival of endemic species through periods of climate change. *Nature Climate Change*, **3**, 1039–1043.
- Belyea, L.R. & Lancaster, J. (1999) Assembly rules within a contingent ecology. *Oikos*, **86**, 402–416.
- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology and Evolution*, **9**, 191–193.
- Brooker, R.W. & Callaghan, T.V. (1998) The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos*, **81**, 196–207.
- Butterfield, B.J., Cavieres, L.A., Callaway, R.M. *et al.* (2013) Alpine cushion plants inhibit the loss of phylogenetic diversity in severe environments. *Ecology Letters*, **16**, 478–486.
- Callaway, R.M., Brooker, R.W., Choler, P., Kikvidze, Z., Lortie, C.J., Michalet, R., Paolini, L., Pugnaire, F.I., Newingham, B., Aschehoug, E.T., Armas, C., Kikodze, D. & Cook, B.J. (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.
- Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.
- Chase, J.M. (2003) Community assembly: when should history matter? *Oecologia*, **136**, 489–498.
- Chase, J.M. (2007) Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences USA*, **104**, 17430–17434.

- Choler, P., Michalet, R. & Callaway, R.M. (2001) Facilitation and competition on gradients in alpine plant communities. *Ecology*, **82**, 3295–3308.
- Cornuault, J., Warren, B.H., Bertrand, J.A.M., Milá, B., Thébaud, C. & Heeb, P. (2013) Timing and number of colonizations but not diversification rates affect diversity patterns in hemisporidian lineages on a remote oceanic archipelago. *The American Naturalist*, **182**, 820–833.
- Donohue, I., Jackson, A.L., Pusch, M.T. & Irvine, K. (2009) Nutrient enrichment homogenizes lake benthic assemblages at local and regional scales. *Ecology*, **90**, 3470–3477.
- Drake, J.A. (1991) Community-assembly mechanics and the structure of an experimental species ensemble. *The American Naturalist*, **137**, 1–26.
- Fukami, T. (2004) Assembly history interacts with ecosystem size to influence species diversity. *Ecology*, **85**, 3234–3242.
- Fukami, T. (2015) Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics*, **46**, in press.
- 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.
- Geange, S.W. & Stier, A.C. (2010) Priority effects and habitat complexity affect the strength of competition. *Oecologia*, **163**, 111–118.
- Gehrke, B. & Linder, H.P. (2011) Time, space and ecology: why some clades have more species than others. *Journal of Biogeography*, **38**, 1948–1962.
- Gelman, A. & Hill, J. (2007) *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, Cambridge, UK.
- Gelman, A. & Pardoe, I. (2006) Bayesian measures of explained variance and pooling in multilevel (hierarchical) models. *Technometrics*, **48**, 241–251.
- Gillespie, R. (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science*, **303**, 356–359.
- Heenan, P.B. & McGlone, M.S. (2013) Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. *New Zealand Journal of Ecology*, **37**, 105–113.
- Herben, T., Suda, J. & Munclinger, P. (2005) The ghost of hybridization past: niche pre-emption is not the only explanation of apparent monophyly in island endemics. *Journal of Ecology*, **93**, 572–575.
- Kardol, P., Souza, L. & Classen, A.T. (2013) Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos*, **122**, 84–94.
- Kéry, M. (2010) *Introduction to WinBUGS for ecologists: a Bayesian approach to regression, ANOVA, mixed models and related analyses*. Academic Press, Burlington, MA.
- Knope, M.L., Forde, S.E. & Fukami, T. (2012) Evolutionary history, immigration history, and the extent of diversification in community assembly. *Frontiers in Microbiology*, **2**, 273.
- Kumar, S. (2005) Molecular clocks: four decades of evolution. *Nature Reviews Genetics*, **6**, 654–662.
- Lee, W.G., Tanentzap, A.J. & Heenan, P.B. (2012) Plant radiation history affects community assembly: evidence from the New Zealand alpine. *Biology Letters*, **8**, 558–561.
- Linder, H.P. (2008) Plant species radiations: where, when, why? *Philosophical Transactions of the Royal Society B: Biological Sciences*, **363**, 3097–3105.
- Lockhart, P.J., McLenachan, P.A., Havell, D., Glenny, D., Huson, D. & Jensen, U. (2001) Phylogeny, radiation, and transoceanic dispersal of New Zealand alpine buttercups: molecular evidence under split decomposition. *Annals of the Missouri Botanical Garden*, **88**, 458–477.
- Losos, J.B., Jackman, T.R., Larson, A., de Queiroz, K. & Rodríguez-Schettino, L. (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**, 2115–2118.
- McGlone, M.S., Duncan, R.P. & Heenan, P.B. (2001) Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *Journal of Biogeography*, **28**, 199–216.
- Patiño, J., Medina, R., Vanderpoorten, A., González-Mancebo, J.M., Werner, O., Devos, N., Mateo, R.G., Lara, F. & Ros, R.M. (2013) Origin and fate of the single-island endemic moss *Orthotrichum handiense*. *Journal of Biogeography*, **40**, 857–868.
- Pirie, M.D., Lloyd, K.M., Lee, W.G. & Linder, H.P. (2010) Diversification of *Chionocholea* (Poaceae) and biogeography of the New Zealand Southern Alps. *Journal of Biogeography*, **37**, 379–392.
- Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P., Olsson, U., Ghosh-Harihar, M., Ishtiaq, F., Gupta, S.K., Martens, J., Harr, B., Singh, P. & Mohan, D. (2014) Niche filling slows the diversification of Himalayan songbirds. *Nature*, **509**, 222–225.
- R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: <http://www.r-project.org/>.
- Richardson, J.E., Bakar, A.M., Tosh, J., Armstrong, K., Smedmark, J., Anderberg, A.A., Slik, F. & Wilkie, P. (2014) The influence of tectonics, sea-level changes and dispersal on migration and diversification of Isonandreae (Sapotaceae). *Botanical Journal of the Linnean Society*, **174**, 130–140.
- Richardson, S. & Gilks, W.R. (1993) A Bayesian approach to measurement error problems in epidemiology using conditional independence models. *American Journal of Epidemiology*, **138**, 430–442.
- Schluter, D. (2000) *The ecology of adaptive radiation*. Oxford University Press, Oxford.
- Schuur, E.A.G. & Matson, P.A. (2001) Net primary productivity and nutrient cycling across a mesic to wet precipitation gradient in Hawaiian montane forest. *Oecologia*, **128**, 431–442.

- Silvertown, J. (2004) The ghost of competition past in the phylogeny of island endemic plants. *Journal of Ecology*, **92**, 168–173.
- Silvertown, J., Francisco-Ortega, J. & Carine, M. (2005) The monophyly of island radiations: an evaluation of niche pre-emption and some alternative explanations. *Journal of Ecology*, **93**, 653–657.
- Stan Development Team (2014) *Stan: a C++ library for probability and sampling*, Version 2.2. Available at: <http://mc-stan.org/>.
- Swenson, N.G. (2011) The role of evolutionary processes in producing biodiversity patterns, and the interrelationships between taxonomic, functional and phylogenetic biodiversity. *American Journal of Botany*, **98**, 472–480.
- Tanentzap, A.J., Lee, W.G. & Coomes, D.A. (2012) Soil nutrient supply modulates temperature-induction cues in mast-seeding grasses. *Ecology*, **93**, 462–469.
- Urban, M.C. & De Meester, L. (2009) Community monopolization: local adaptation enhances priority effects in an evolving metacommunity. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4129–4138.
- Vannette, R.L. & Fukami, T. (2014) Historical contingency in species interactions: towards niche-based predictions. *Ecology Letters*, **17**, 115–124.
- Wardle, P. (1963) Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. *New Zealand Journal of Botany*, **1**, 3–17.
- Winkworth, R.C., Wagstaff, S.J., Glenny, D. & Lockhart, P.J. (2005) Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organisms Diversity and Evolution*, **5**, 237–247.

## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Posterior distributions of alternative model parameters.

## BIOSKETCH

**Devin R. Leopold** is a PhD student in the Fukami Lab in the Department of Biology, Stanford University, California. The authors are working to understand the role of evolutionary priority effects in the diversification and community structure of New Zealand plants.

Author contributions: D.R.L. led the analysis with significant input from T.F., W.G.L. and A.J.T.; P.J.H. and A.J.T. compiled the phylogenetic data; D.R.L. wrote the original manuscript and all authors contributed to revisions.

---

Editor: James Richardson