

# Precipitation alters the strength of evolutionary priority effects in forest community assembly of pteridophytes and angiosperms

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## Summary

**1.** The ecological conditions promoting evolutionary priority effects, where the order and timing of ancestral species arrival into a new habitat influences extant community assembly, are poorly understood. Studies in the New Zealand alpine indicated that early-arriving angiosperm lineages dominated communities via niche pre-emption. Forests have a much longer (>60 myr) evolutionary history in New Zealand than alpine communities (<2 myr) and greater structural complexity.

**2.** Here we ask whether community effects of arrival order persist in cool temperate forest communities in southern New Zealand that have assembled throughout the Cenozoic. Combining phylogenetically derived clade ages and forest vegetation data from across a mountain range, we compare effects of clade age on relative richness and abundance of two taxonomic groups (pteridophytes and angiosperms) along precipitation gradients.

**3.** We show that older clades of both groups tended to have greater relative abundance and older angiosperm clades had greater relative richness. Relative richness and abundance also increased with regional clade diversity, independent of clade age.

**4.** The strength of the clade age effect on community dominance changed differently along precipitation gradients depending on the response and taxonomic group. Clade age had a stronger effect on relative abundance of pteridophytes with increasing elevation and westerliness (i.e. as precipitation increased). In contrast, the effect of clade age on relative abundance of angiosperms decreased with westerliness. Precipitation did not alter the clade age effect on relative richness.

**5. Synthesis.** We show that evolutionary priority effects persist in communities with a longer evolutionary history than has been investigated to date and across physiologically contrasting taxonomic groups, suggesting priority effects are general drivers of community assembly over macro-evolutionary time-scales. Furthermore, the strength of evolutionary priority effects attenuated along a gradient of decreasing resources, at least for pteridophytes, which improves our ability to predict conditions in which the arrival order of lineages influences community assembly.

**Key-words:** clade age, community assembly, community dominance, determinants of plant community diversity and structure, environmental gradients, historical contingency, immigration history, radiations, Stress Gradient Hypothesis

## Introduction

Stephen Jay Gould famously asked whether evolution would have created a different biotic world were the 'tape of life' to

be rewound and played again (Gould 1989). One type of such historical contingency is priority effects, where the order and timing of species arrival into a local community affect the resulting community structure and function (Fukami 2015). Priority effects have been documented across many ecosystems and taxonomic groups (e.g., Almany 2004; Fukami 2004; Weslien *et al.* 2011; Hernandez & Chalcraft 2012), where early-arriving taxa often dominate the resulting

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communities (Körner *et al.* 2008; Fukami *et al.* 2010; von Gillhaussen *et al.* 2014). Over longer time periods, the interplay between ecological and evolutionary processes during community assembly can lead to evolutionary priority effects, where occupation of niche space by early-arriving lineages that subsequently diversify precludes establishment, dominance and/or diversification of later arrivals (Silvertown 2004; Silvertown, Francisco-Ortega & Carine 2005; Tanentzap *et al.* 2015; De Meester *et al.* 2016). Evolutionary priority effects have been identified in multiple types of communities, including bacteria (Fukami *et al.* 2007; Knope, Forde & Fukami 2012), lizards (Losos *et al.* 1998) and alpine angiosperms (Lee, Tanentzap & Heenan 2012; Leopold *et al.* 2015; Tanentzap *et al.* 2015). However, it remains poorly understood how pervasive evolutionary priority effects may be across different ecological conditions and taxonomic groups.

Because evolutionary priority effects operate via niche pre-emption by early-arriving lineages (Silvertown 2004; Silvertown, Francisco-Ortega & Carine 2005), they may diminish over time and in ecosystems with greater structural complexity. The New Zealand alpine, where we previously found evidence for evolutionary priority effects (Lee, Tanentzap & Heenan 2012; Leopold *et al.* 2015; Tanentzap *et al.* 2015), is a relatively young bioclimatic zone (<2 myr; Heenan & McGlone 2013), whereas neighbouring forests have persisted throughout the Cenozoic (>60 myr; Lee, Lee & Mortimer 2001; Lee *et al.* 2012, 2016). New Zealand forests experienced dramatic changes during the late Cenozoic, with range contraction during partial marine inundation in the Oligocene (Mildenhall *et al.* 2014 and references therein) followed by cooling and climate shifts through the Pliocene–Pleistocene, collectively causing extinction across many forest lineages (Lee, Lee & Mortimer 2001; Lee *et al.* 2016). Major disturbances and extinctions may create ecological opportunity for both *in situ* taxa and immigrants by opening up niche space, thus reducing the advantage conferred by early arrival of ancestors and weakening priority effects (cf. Tanentzap *et al.* 2015). The vertical structure of forests may also create a range of different niches than observed in alpine communities, providing ecological opportunity for lineages not observed in the alpine zone, such as a number of pteridophytes (Table 1). Forest trees simultaneously modify an important resource axis (light availability) and provide substrate for recruitment of epiphytes and understorey plants, both processes which may increase niche diversity and promote diversification of plant lineages (Schneider *et al.* 2004; Coomes *et al.* 2005, 2009; Schuettpelz & Pryer 2009). For these reasons, evolutionary priority effects may be weaker in forests than in alpine communities.

Priority effects operating via competition are likely to attenuate along gradients of abiotic stress, as the predominance of competitive interactions in benign environments shifts to facilitative interactions in harsh environments (Stress Gradient Hypothesis; Bertness & Callaway 1994). Stronger ecological priority effects have been observed in more benign or resource-rich environments for pond communities (Chase 2007), plant communities (Ejrnæs, Bruun & Graae 2006;

Kardol, Souza & Classen 2013; Plücker *et al.* 2013) and nectar yeasts (Vannette & Fukami 2014). Similarly, alpine plant community dominance by early-arriving clades diminished along environmental gradients corresponding to temperature and soil saturation stress (Leopold *et al.* 2015), demonstrating that ecological processes mediate the influence of evolutionary priority effects on community assembly. As in the New Zealand alpine zone (Tanentzap, Lee & Coomes 2012), temperature decreases with increasing elevation in montane forests, but at a much lower rate. Gradients of increasing precipitation with elevation and from east to west in South Island, New Zealand (Wratt *et al.* 2000), may thus be more informative to predicting conditions in which arrival order of plant lineages will influence community assembly in forests by providing a steeper environmental gradient than temperature. Furthermore, pteridophytes and angiosperms may respond differently to precipitation gradients given that ferns generally have greater water requirements than angiosperms due in part to stomatal differences leading to lower water-use efficiency (McAdam & Brodrigg 2012). New Zealand forests thus provide an ideal system to determine whether evolutionary priority effects consistently influence community assembly across physiologically contrasting taxonomic groups.

Here we investigate priority effects resulting from tens of millions of years of immigration history in cool temperate forest communities of southern New Zealand. The aim was to improve predictions of when evolutionary priority effects will have the strongest effect on extant community structure, thus expanding upon previous work in alpine plant communities (Lee, Tanentzap & Heenan 2012; Leopold *et al.* 2015; Tanentzap *et al.* 2015). If evolutionary priority effects occur, we expect that early-arriving lineages will pre-empt niche space and thus be more dominant in extant communities (Tanentzap *et al.* 2015; De Meester *et al.* 2016). Dated phylogenies are available to estimate the timing of divergence for many taxa from their nearest relatives outside New Zealand (Table 1), allowing us to approximate the order of arrival of ancestral taxa and thus the immigration timing of extant forest lineages (*sensu* Gehrke & Linder 2011; Cornuault *et al.* 2013; Hennequin *et al.* 2014). We ask the following questions: (i) do evolutionary priority effects occur in forest communities with similar strength to those observed in alpine communities?, and (ii) does the strength of evolutionary priority effects in forests attenuate along environmental gradients as precipitation decreases in accordance with the Stress Gradient Hypothesis?

## Materials and methods

We used data collected from below treeline across the Murchison Mountains, South Island, New Zealand (45°15' S, 167°33' E), in the austral summer November 1980 – January 1981. Forest community data were collected from 340 10 × 10 m plots located across 63 transects arranged in a stratified random sampling design (Wilson & Lee 1994; Bee *et al.* 2009), in which per cent areal cover of each plant species present in the plot was visually estimated and total cover was allowed to sum to >100% for overlapping canopies. Each transect spanned an elevation gradient from valley floor to treeline, with plots

**Table 1.** Stem ages (millions of years) for the 38 focal clades in forest plots in the Murchison Mountains, with uncertainty estimates of  $\pm$  SD or (95% HPD interval) as provided by the listed references. Stem age represents the divergence time between the New Zealand clade and its nearest extant relative outside New Zealand. Regional clade diversity is the total number of species in each focal clade observed across all 340 forest plots

Taxonomic group	Clade, with generic naming authority	Stem age (myr)	Stem age references	Regional clade diversity
Pteridophyte	<i>Asplenium</i> L.*	13.91 (19.31–8.60)	Papadopulos <i>et al.</i> (2011); A. S. T. Papadopulos, 2015, pers. comm.	2
	<i>Cyathea</i> Sm.*	48.00 (60.00–35.00)	Korall & Pryer (2014)	2
	<i>Hymenophyllum</i> Sm.	32.77 $\pm$ 8.93 <sup>†</sup>	Perrie & Brownsey (2007)	10
	<i>Hypolepis</i> Bernh.	12.67 $\pm$ 7.03 <sup>†</sup>	Perrie & Brownsey (2007)	1
	<i>Leptopteris</i> C.Presl	12.00 $\pm$ 8.03 <sup>†</sup>	Perrie & Brownsey (2007)	1
	<i>Lycopodium</i> L.	4.60 $\pm$ 4.97 <sup>†</sup>	Perrie & Brownsey (2007)	2
	<i>Microsorium</i> Link	13.70 $\pm$ 4.33 <sup>†</sup>	Perrie & Brownsey (2007)	1
	<i>Notogrammitis</i> Parris	14.70 (18.60–10.70)	Sundue <i>et al.</i> (2014)	4
	<i>Polystichum</i> Roth	15.30 (25.69–6.76)	Papadopulos <i>et al.</i> (2011); A. S. T. Papadopulos, 2015, pers. comm.	1
	<i>Tmesipteris</i> Bernh.	8.07 $\pm$ 4.83 <sup>†</sup>	Perrie & Brownsey (2007)	1
Angiosperm	<i>Anisotome</i> Hook.f.	9.36 (16.90–3.51) <sup>†</sup>	Spalik <i>et al.</i> (2010); Nicolas & Plunkett (2014)	2
	<i>Aristotelia</i> L'Hér.	17.00 $\pm$ 1.00	Crayn, Rossetto & Maynard (2006)	2
	<i>Astelia</i> Banks & Sol. ex R.Br. (subgenus <i>Tricella</i> )*	15.40 (25.30–6.90)	Birch & Keeley (2013)	2
	<i>Astelia</i> Banks & Sol. ex R.Br. ( <i>A. linearis</i> clade)*	3.70 (9.00–1.50)	Birch & Keeley (2013)	1
	<i>Chionochloa</i> Zotov	19.95 (23.60–16.65) <sup>†</sup>	Antonelli <i>et al.</i> (2010); Pirie <i>et al.</i> (2012)	5
	<i>Coprosma</i> J.R.Forst. & G.Forst.	12.13 (17.41–7.44)	Papadopulos <i>et al.</i> (2011); A. S. T. Papadopulos, 2015, pers. comm.	16
	<i>Craspedia</i> G.Forst.	3.10 $\pm$ 0.60 <sup>†</sup>	Ford <i>et al.</i> (2007); K. A. Ford, 2011, pers. comm.	1
	<i>Dracophyllum</i> Labill.	6.80 (9.68–5.57) <sup>†</sup>	Wagstaff <i>et al.</i> (2010)	3
	<i>Elaeocarpus</i> L.	21.00 $\pm$ 1.00	Crayn, Rossetto & Maynard (2006)	1
	<i>Forstera</i> L. ex G.Forst. – <i>Phyllachne</i> Forst. & Forst.	6.32 $\pm$ 1.10	Wagstaff & Wege (2002)	2
	<i>Fuscospora</i> (R.S.Hill & J.Read) Heenan & Smissen	16.10 (30.00–4.60)	Sauquet <i>et al.</i> (2012)	3
	<i>Gaultheria</i> Kalm ex L.	14.46 (22.40–6.89)	Schwery <i>et al.</i> (2015)	4
	<i>Gentianella</i> Moench	2.05 $\pm$ 0.85 <sup>†</sup>	von Hagen & Kadereit (2001)	1
	<i>Griselinia</i> J.R.Forst. & G.Forst.	12.14 (25.43–2.57)	Nicolas & Plunkett (2014)	1
	<i>Hoheria</i> A.Cunn.	14.95 (20.40–7.60) <sup>†</sup>	Wagstaff & Tate (2011)	1
	<i>Hydrocotyle</i> L.	8.33 (14.37–2.96)	Nicolas & Plunkett (2014)	2
	<i>Leptecophylla</i> C.M. Weiller	1.89 (3.18–0.87) <sup>†</sup>	Puente-Lelièvre <i>et al.</i> (2013)	1
	<i>Metrosideros</i> Banks ex Gaertn. ( <i>umbellata</i> clade)*	24.63 (38.06–12.83)	Papadopulos <i>et al.</i> (2011); A. S. T. Papadopulos, 2015, pers. comm.	1
	<i>Metrosideros</i> Banks ex Gaertn. ( <i>diffusa</i> clade)*	29.06 (43.93–14.92)	Papadopulos <i>et al.</i> (2011); A. S. T. Papadopulos, 2015, pers. comm.	1
	<i>Nertera</i> Banks & Sol. ex Gaertn.	3.47 (6.43–0.92)	Papadopulos <i>et al.</i> (2011); A. S. T. Papadopulos, 2015, pers. comm.	4
	<i>Olearia</i> Moench (macrocephalous)*	4.70 (8.40–2.40)	Wagstaff, Breitwieser & Ito (2011)	1
	<i>Olearia</i> Moench (other)*	8.10 (12.40–4.90)	Wagstaff, Breitwieser & Ito (2011)	6
	<i>Poa</i> L.*	3.55 (5.50–1.80) <sup>†</sup>	Birch <i>et al.</i> (2014)	4
	<i>Pseudopanax</i> K.Koch	9.91 (15.92–4.81)	Nicolas & Plunkett (2014)	3
	<i>Pseudowintera</i> Dandy	45.18 (58.78–33.18)	Thomas <i>et al.</i> (2014)	1
	<i>Ranunculus</i> L.*	5.05 $\pm$ 0.84	Lockhart <i>et al.</i> (2001)	4
	<i>Raukaua</i> Seem.	9.46 (17.65–3.12)	Nicolas & Plunkett (2014)	2
	<i>Veronica</i> L.	10.21 (13.33–7.21)	Meudt <i>et al.</i> (2015)	7

\*Subgeneric clade age used because genus is not monophyletic in New Zealand.

<sup>†</sup>Reported clade age and uncertainty were averaged from multiple estimates within and/or among listed references.

randomly located at approximately 100-m elevation intervals and within 50 m of the transect. Plot size was chosen to best capture abundance of all plant species (forest floor herbs to canopy trees) while minimizing investigator error in estimating per cent cover. Richness of forest plots ranged from 3 to 51 species (mean of  $16.6 \pm 7.0$  SD), and adult tree DBH rarely exceeded 1 m in

permanent forest plots throughout the same mountain range (Tanentzap *et al.* 2009), and thus, it was unlikely for a single tree to exclude all other species from a plot. The plant communities within the data set consisted almost exclusively of indigenous species, with one occurrence of a wilding pine seedling (*Pinus contorta*) being the sole non-native species observed out of a total of 5653 recordings.

The data set spanned two environmental gradients: an elevation gradient of 186–1170 m above sea level (a.s.l.) and an east-to-west precipitation gradient of ca. 2300–6700 mm year<sup>-1</sup> (mean annual rainfall from Takahe Valley and Wilmot Pass stations; National Institute of Water and Atmospheric Research 2014). Mean monthly temperatures range from ca. 3.6 °C in July to 14.1 °C in January/February at 180 m a.s.l. and from 0.7 °C in July to 9.7 °C in January/February at 1140 m a.s.l. (monthly temperature data from 22 stations in the Fiordland region spanning 178–1140 m a.s.l.; National Institute of Water and Atmospheric Research 2014). Thus, mean monthly temperature decreases approximately 0.13 °C on average per 100-m elevation gain, compared to 0.98 °C per 100 m a.s.l. in the alpine zone (Tanentzap, Lee & Coomes 2012). As observed in the Southern Alps (Wratt *et al.* 2000), precipitation increases with elevation for a given longitude; for example, mean annual rainfall at Deep Cove stations (<10 m a.s.l.) is ca. 1200 mm year<sup>-1</sup> lower than observed at Wilmot Pass (671 m a.s.l.; National Institute of Water and Atmospheric Research 2014).

We focused our analysis on 38 generic or subgeneric clades in two groups (pteridophytes and angiosperms) for which time-calibrated molecular phylogenies have been published, with the additional criteria that they were not monotypic in New Zealand and they occurred in at least four plots in the data set (Table 1; see Table S1 in Supporting Information). To estimate immigration timing, we used the divergence time between the most recent common ancestor of the New Zealand clade and its nearest extant relative outside New Zealand (i.e. stem age). We compiled these stem age estimates and their uncertainty from sources using a variety of sequence regions and molecular clock methods (Table 1). We estimated a variance for each of the stem ages using the standard deviation (SD) or the longer of the two tails of the 95% highest posterior density interval of the stem age estimate, depending on what was reported (*sensu* Lee, Tanentzap & Heenan 2012). Due to insufficient data to compare taxonomic groups, we did not use crown age (i.e. age of the most recent common ancestor of the New Zealand clade) as an estimate of immigration timing. Furthermore, crown age may underestimate residence time of a lineage if there is a lag between arrival of an ancestral taxon and radiation of the clade. Because stem and crown ages were positively correlated in the 21 clades for which both were available ( $r = 0.56$ ,  $P = 0.004$  from a one-tailed test), we expect they would produce similar results.

For each clade, we quantified two estimates of community dominance in each plot  $j$  in which clade  $i$  was observed. Relative richness  $R_{ij}$  was quantified as the proportion of the total species richness in a plot represented by a clade and relative abundance  $A_{ij}$  was the proportion of total per cent cover. We estimated clade richness across the Murchison Mountains ('regional clade diversity') as the total number of species within each clade observed in the forest data set (Table 1).

We used linear models estimated within a Bayesian framework to test our hypotheses about how community dominance varied with clade age across the two taxonomic groups. We allowed clade age effects  $\beta_k^{(1)}$  to vary between pteridophytes and angiosperms to test whether priority effects were consistent across taxonomic group  $k$  with contrasting physiology. Though clade richness and abundance sometimes exhibit nonlinear relationships over time (e.g. pteridophyte richness and abundance peaked prior to the Cretaceous, then declined (Schneider *et al.* 2004)), there is little evidence across the tree of life that extant clade richness peaks at intermediate clade age (Rabosky, Slater & Alfaro 2012). Including a quadratic term did not improve the predictive ability of our models of community dominance [i.e. there was no difference in the leave-one-out cross-validation

information criterion (Vehtari, Gelman & Gabry 2016)]; thus, we only included a linear term. We also tested whether the effect of clade age increased with elevation and westerliness to determine whether priority effects attenuated along expected resource gradients (i.e. weaker under drier conditions). We included regional clade diversity  $s_i$  as a predictor to control for the possibility that species within more diverse clades may co-occur more frequently or with greater cover than with non-focal clades because of greater diversity. To allow for clades to differ in community dominance due to differences in individual plant size, we included the maximum height  $h_i$  of the clade's species that occurred in Murchison Mountain forests (Table S1). We did not expect the effect of regional clade diversity nor height to differ between groups. To predict the logit transformation of  $R_{ij}$ , which accounted for the fact that proportions are bounded and produce non-normal errors, our model therefore took the form:

$$\text{logit}(R_{ij}) \sim N(\mu_{ij}, \sigma_i).$$

$$\mu_{ij} = \alpha_k + \beta_k^{(1)} \ln(t_i) + \beta_k^{(2)} z_j + \beta_k^{(3)} p_j + \beta_k^{(4)} \ln(t_i) \times z_j + \beta_k^{(5)} \ln(t_i) \times p_j + \gamma \ln(s_i) + \eta h_i + \varepsilon_j, \quad \text{eqn 1}$$

where  $\alpha_k$  is the mean relative clade richness,  $\beta_k^{(2)}$  is the effect of elevation  $z_j$ ,  $\beta_k^{(3)}$  is the effect of westerliness  $p_j$ ,  $\beta_k^{(4)}$  and  $\beta_k^{(5)}$  are the changes in the effect of clade age with increasing elevation and westerliness, respectively,  $\gamma$  is the effect of regional clade diversity  $s_i$ , and  $\eta$  is the effect of maximum clade height  $h_i$ . We included  $\varepsilon_j$  to account for unexplained plot-level variation. We propagated uncertainty associated with mean published estimates of clade age into eqn 1 as  $\sigma_i = \sqrt{(\tau_i(\beta_k^{(1)} + \beta_k^{(4)} z_j + \beta_k^{(5)} p_j)/t_i)^2 + \sigma^2}$ , where  $\tau_i$  and  $\sigma$  are the observed SD for each clade  $i$  derived from published studies and an estimated residual SD, respectively (*sensu* Tanentzap *et al.* 2015). To predict relative clade abundance, we refitted eqn 1 using  $A_{ij}$ .

All analyses were conducted by calling STAN v. 2.7.0 (Stan Development Team 2015) using the RSTAN library in R v. 3.2.2 (R Core Team 2015). We assigned uninformative priors for model parameters:  $\sim N(0, 100)$  for regression coefficients and  $\sim U(0, 40)$  for SD. All predictors were standardized to a mean of 0 and SD of 1 so that estimated effects represented a change in the response with 1 SD change in the predictor. Three MCMC chains of 6000 iterations were simulated with a burn-in of 2000 runs and thinning of 8. Convergence of the chains was confirmed by visual inspection of parameter traces and scale reduction factors <1.01, and independence of simulations was confirmed by ensuring all fixed-effect parameters had an effective sample size >1000 (Gelman & Hill 2007). We assessed model fit using two metrics: a posterior predictive check of the proportion of model iterations where the sums of squared model residuals from the data were greater than from simulated data drawn from the modelled distribution (with Bayes  $P \approx 0.5$  for a good fit to the data), and a Bayesian  $R^2$  statistic analogous to the proportion of variance explained in classical regression (Gelman & Hill 2007).

Model parameter effects were inferred by calculating posterior means and 95% credible intervals (CIs) from the combined net output of all three chains (1500 samples total from the posterior distribution) and supported our hypotheses if means were in the predicted direction and the 95% CIs excluded zero. We used the following predictions to address our two research questions: (i) if evolutionary priority effects occur in forest communities, we expect a positive effect of clade age on relative richness and relative abundance, and (ii) if priority effects are stronger with greater resource abundance (i.e. in wetter

conditions), we expect a positive interaction between clade age and both elevation and westerliness.

## Results

### DOES CLADE AGE POSITIVELY CORRELATE WITH COMMUNITY DOMINANCE?

Older angiosperm clades had greater relative richness and older pteridophyte and angiosperm clades had greater relative abundance in forest communities, when accounting for the potential for tree clades to be more dominant simply because of their larger size compared to herbaceous clades (Table 2, Fig. 1). Clade age did not influence relative clade richness of pteridophytes (Table 2, Fig. 1a). Regional clade diversity was positively correlated with both relative richness and relative abundance (Table 2). Correlations between clade age and regional clade diversity effects in the posterior were generally

weak and sometimes non-existent ( $r < |0.34|$ ). Thus, though clade age and regional clade diversity both contributed to greater relative abundance, this was not simply a result of age influencing diversity.

### DOES THE STRENGTH OF EVOLUTIONARY PRIORITY EFFECTS ATTENUATE WITH DECREASING PRECIPITATION?

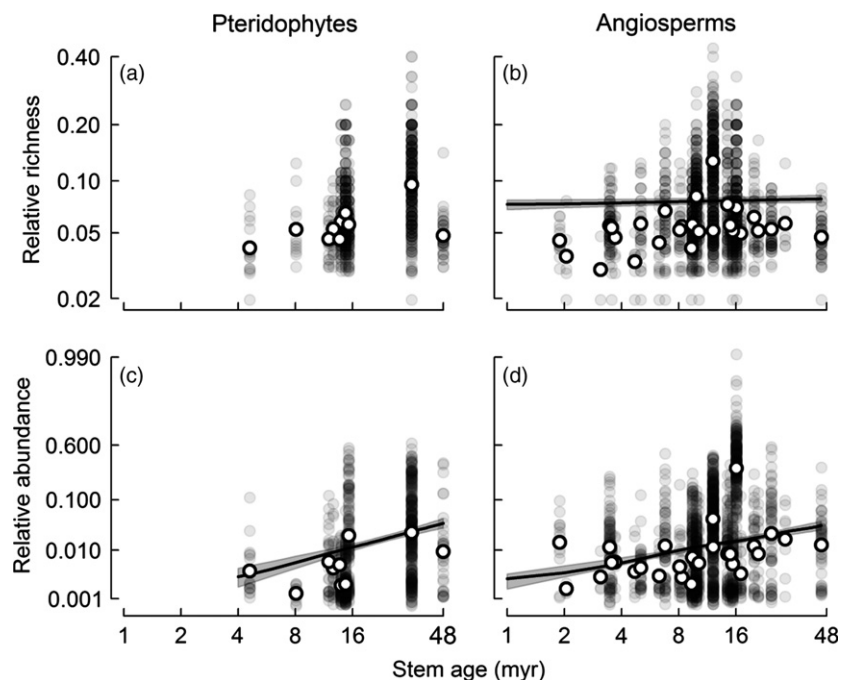
The effect of clade age on relative abundance of pteridophytes increased with elevation, according to our prediction (Table 2, Fig. 2c). Clade age and elevation did not interact to affect relative abundance of angiosperms or relative clade richness of either taxonomic group (Table 2, Fig. 2). Relative richness of both taxonomic groups increased with elevation, but relative abundance of pteridophytes declined with elevation (Table 2).

The effect of clade age on relative abundance of pteridophytes increased with westerliness, according to our prediction

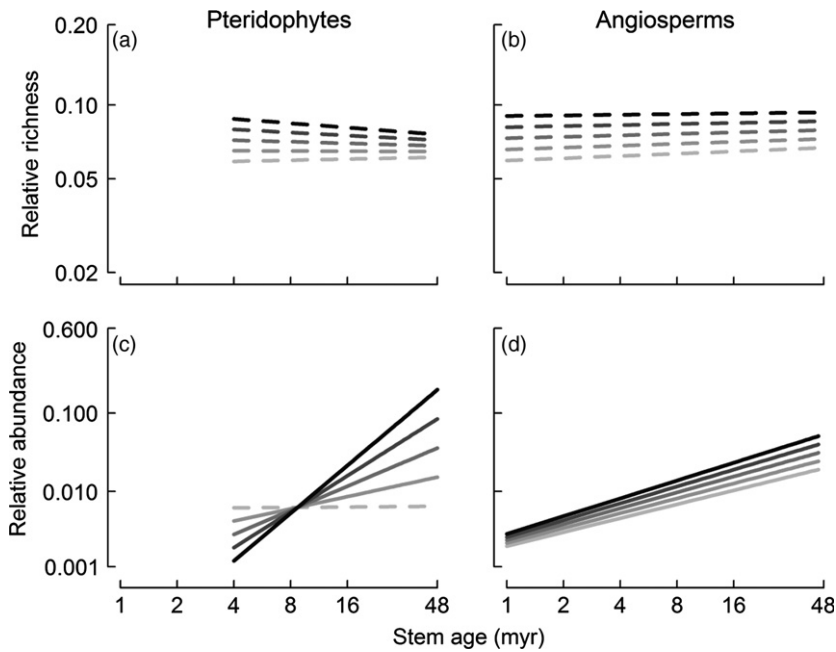
**Table 2.** Mean parameter estimates (with 95% credible intervals) for models of community dominance of pteridophyte and angiosperm clades in forest plots of the Murchison Mountains, New Zealand

	Relative richness		Relative abundance	
	Pteridophytes	Angiosperms	Pteridophytes	Angiosperms
Intercept ( $\alpha$ )	<b>-2.53 (-2.64 to -2.42)</b>	<b>-2.54 (-2.61 to -2.47)</b>	<b>-7.33 (-8.13 to -6.58)</b>	<b>-6.09 (-6.44 to -5.73)</b>
Clade age ( $\beta^{(1)}$ )	-0.01 (-0.03 to 0.006)	<b>0.01 (0.0006 to 0.03)</b>	<b>0.58 (0.45 to 0.72)</b>	<b>0.39 (0.31 to 0.47)</b>
Elevation ( $\beta^{(2)}$ )	<b>0.13 (0.02 to 0.25)</b>	<b>0.10 (0.03 to 0.18)</b>	<b>-1.05 (-1.71 to -0.37)</b>	0.09 (-0.22 to 0.41)
Westerliness ( $\beta^{(3)}$ )	<b>-0.27 (-0.38 to -0.17)</b>	<b>-0.14 (-0.22 to -0.07)</b>	-0.59 (-1.22 to 0.09)	<b>0.74 (0.45 to 1.03)</b>
Clade age $\times$ elevation ( $\beta^{(4)}$ )	-0.01 (-0.03 to 0.008)	-0.003 (-0.02 to 0.01)	<b>0.27 (0.15 to 0.39)</b>	0.02 (-0.04 to 0.09)
Clade age $\times$ westerliness ( $\beta^{(5)}$ )	0.01 (-0.005 to 0.03)	-0.01 (-0.03 to 0.0007)	<b>0.14 (0.02 to 0.27)</b>	<b>-0.17 (-0.23 to -0.11)</b>
Regional clade diversity ( $\gamma$ )	<b>0.25 (0.24 to 0.26)</b>		<b>0.50 (0.43 to 0.57)</b>	
Maximum height ( $\eta$ )	-0.01 (-0.03 to 0.005)		<b>1.06 (0.97 to 1.14)</b>	

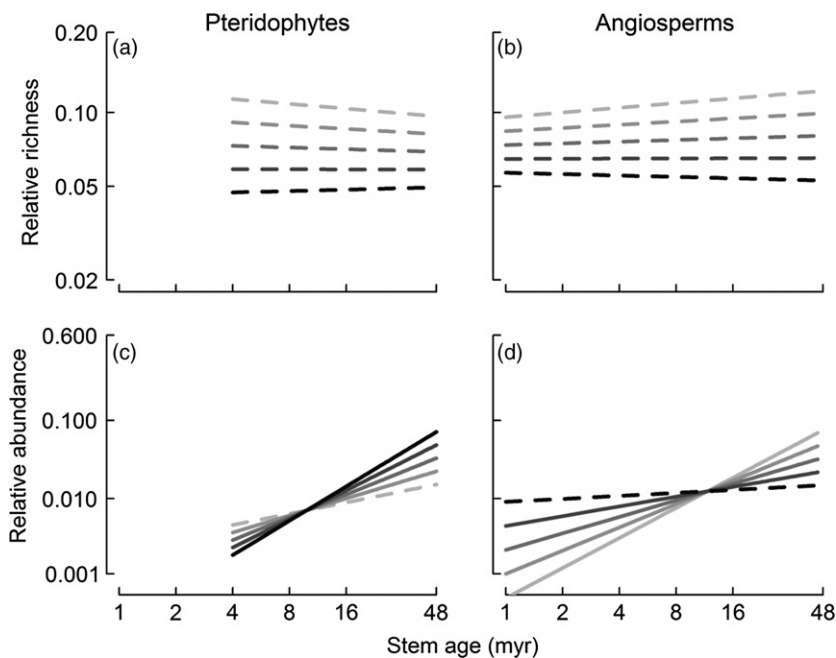
Bolded values have 95% CIs that exclude zero.



**Fig. 1.** Community dominance in relation to clade age of (a, c) pteridophytes and (b, d) angiosperms in forests of the Murchison Mountains, New Zealand, quantified as (a, b) relative clade richness and (c, d) relative clade abundance. Light grey circles are responses for each focal plant clade in each plot ( $n = 2746$ ); white circles are clade means ( $n = 38$ ). Solid lines indicate mean relationships, with 95% credible intervals indicated by grey polygons.



**Fig. 2.** Predicted mean relationships between clade age and community dominance of (a, c) pteridophytes and (b, d) angiosperms at five intervals of elevation from the range of the Murchison Mountains forest data set (186–1170 m a.s.l., light grey to black; solid lines indicate a nonzero slope, and dashed lines indicate the 95% CI for the slope overlaps zero). Community dominance was quantified as (a, b) relative clade richness and (c, d) relative clade abundance. Trendlines derived from 1500 posterior samples of the model.



**Fig. 3.** Predicted mean relationships between clade age and community dominance of (a, c) pteridophytes and (b, d) angiosperms at five intervals of location from east to west in the Murchison Mountains forest data set (light grey to black; solid lines indicate a nonzero slope, and dashed lines indicate the 95% CI for the slope overlaps zero). Community dominance was quantified as (a, b) relative clade richness and (c, d) relative clade abundance. Trendlines derived from 1500 posterior samples of the model.

(Table 2, Fig. 3c). However, contrary to our prediction, the effect of clade age on relative abundance of angiosperms decreased with westerliness (Table 2, Fig. 3d). Clade age and westerliness did not interact to affect relative richness of either taxonomic group (Table 2, Fig. 3). Relative richness of both groups decreased with westerliness, while relative abundance of angiosperms increased with westerliness (Table 2).

#### MODEL FIT

The posterior predictive check suggested our models fit the data well (Bayes  $P = 0.47$  for the richness model and 0.50 for the abundance model). Our model for relative richness

explained over half the variance in the data (Bayesian  $R^2 = 0.68$ ), while the relative abundance model explained over one-third of the variance (Bayesian  $R^2 = 0.35$ ).

#### Discussion

We found evidence for evolutionary priority effects within both pteridophytes and angiosperms in New Zealand forests, an evolutionarily older and more structurally complex plant community than has been investigated to date. Older pteridophyte clades were more dominant in terms of their relative abundance, and older angiosperm clades were more dominant in terms of both relative richness and relative abundance, as

we previously observed in the alpine zone (Lee, Tanentzap & Heenan 2012; Leopold *et al.* 2015; Tanentzap *et al.* 2015). The effect size of clade age on community dominance of angiosperms in forests (95% CI on relative richness: 0.0006–0.03, 95% CI on relative abundance: 0.31–0.47; Table 2) appears smaller than for local alpine communities (95% CI: 0.13–0.21 and 0.43–1.59, respectively, estimated using an identical modelling approach; Leopold *et al.* 2015), providing some support to our prediction that evolutionary priority effects would be weaker in forests than the alpine zone.

We found that clades with a greater number of species in forest communities of the Murchison Mountains tended to be more dominant, while no effect of regional clade diversity was observed in the alpine zone (Lee, Tanentzap & Heenan 2012; Leopold *et al.* 2015). Previous work has shown both clade diversity and niche availability to increase with clade age for plant lineages in the alpine zone, indicating that residence time promotes diversification and niche occupancy, with both processes leading to community dominance (Tanentzap *et al.* 2015). Importantly, however, we observed independent effects of clade age and regional clade diversity on relative clade richness and abundance in forests, suggesting that dominance of early-arriving clades is at least partly the result of evolutionary priority effects rather than solely a greater residence time over which to diversify.

We found support for our prediction that the strength of evolutionary priority effects would attenuate along a gradient of decreasing resources, where the effect of clade age on relative abundance of pteridophytes tended to weaken with decreasing precipitation (i.e. decreasing elevation and westerliness). These results are consistent with other systems where the strength of priority effects is reduced in harsh or resource-limited environments compared to benign environments (Chase 2007; Kardol, Souza & Classen 2013; Vannette & Fukami 2014; Leopold *et al.* 2015), and suggest that competition plays a lesser role in community assembly in harsher environments. Thus, environmental conditions can mediate the influence of evolutionary priority effects on community assembly.

Contrary to our prediction, the effect of clade age on angiosperm relative abundance weakened with increasing westerliness and was positive throughout the elevation range at which forests occur in the Murchison Mountains. Physiological differences between pteridophytes and angiosperms, such as greater water requirements for ferns, may partly explain contrasting effects of clade age on community dominance of each group across precipitation gradients. Moreover, because multiple abiotic factors vary across the westerliness and elevation gradients we examined, it is possible that angiosperms are responding to a different type of stress gradient than pteridophytes. For example, soil saturation and reduced phosphorous in areas with high precipitation may limit angiosperms more than conifers (Coomes *et al.* 2005), and conifer richness and abundance increased from east-to-west in our data set (see Table S2 and Fig. S1). Additionally, increasing pteridophyte abundance with westerliness (Table S2 and Fig. S1) may lead to reduced light availability

(Coomes *et al.* 2005, 2009), which is more likely to limit angiosperm than pteridophyte recruitment given the higher shade tolerance in many ferns (Kawai *et al.* 2003; Coomes *et al.* 2005). Our results do not support a role for decreasing temperature to weaken priority effects as found in the alpine zone (Leopold *et al.* 2015), perhaps due to the shallower gradient of decreasing temperature with increasing elevation in forests compared to the alpine zone and the buffering of understorey vegetation by canopy trees.

The evolutionary time-scale of this study precludes our ability to test experimentally the existence of priority effects by rewinding Gould's tape and switching the order of arrival of plant lineages (*sensu* Fukami *et al.* 2007). Our previous work modelling the causal relationships between arrival time, lineage diversification and niche occupancy in alpine plants (Tanentzap *et al.* 2015) supports our proposed mechanism of priority effects via niche pre-emption (Silvertown 2004; Silvertown, Francisco-Ortega & Carine 2005; Fukami 2015). However, it is possible that the dominant lineages in our forest data set would dominate regardless of their immigration timing, such as if competitive ability of ancestral taxa were correlated with clade age. Empirical work shows mixed evidence for greater competitive ability among extant taxa of early- versus later-arriving plant lineages in southern beech forests of New Zealand. One species of *Pseudowintera*, the oldest angiosperm focal clade in our data set, has a greater sapling growth rate than *Fuscospora cliffortioides* in very low light (1% of daylight), but this trend reverses at light levels of 30% (Coomes *et al.* 2009). Typical subcanopy angiosperm trees (e.g. *Griselinia* and *Pseudopanax* spp.) in clades younger than *Pseudowintera* and *Fuscospora* intercept more light due to their broader leaves, but tree ferns (e.g. *Cyathea* spp.) intercept the most light (Coomes *et al.* 2005, 2009). Thus, extant species in both early- and late-arriving clades can have strong effects on light-dependent regeneration on the forest floor (i.e. strong competitive effects). Further work examining niche distributions and competitive ability among plant lineages in both the alpine and forest zones of New Zealand, and conducting ancestral reconstructions of these traits, should provide additional mechanistic support for evolutionary priority effects in these communities. These studies would take us closer to answering Gould's question on the role of evolutionary history in producing the contemporary biotic world.

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## Data accessibility

The complete data set for the Murchison Mountains Vegetation Plots 1980–1981 is archived in the New Zealand National Vegetation Survey Databank (<https://nvs.landcareresearch.co.nz/Data/DatasetDetails/4478/28295>; Lee 1980).

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## Supporting Information

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

**Fig. S1.** Plot richness and abundance of taxonomic groups in relation to westerliness.

**Table S1.** New Zealand diversity, plot occurrence, and height of focal clades in Murchison Mountain forests.

**Table S2.** Elevation and westerliness effects on plot richness and abundance of pteridophytes, conifers, and angiosperms.