New Phytologist

Research

Evolutionary priority effects persist in anthropogenically created habitats, but not through nonnative plant invasion

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Received: *28 January 2017*
Accepted: *22 February 2017*

New Phytologist (2017) **215:** 865–876
doi: 10.1111/nph.14544

Key words: anthropogenic disturbance, community assembly, immigration timing, nonnative species, plant radiations, priority effects, soil resource availability, stress gradient hypothesis.

Summary

- Evolutionary priority effects, where early-arriving lineages occupy niche space via diversification and preclude dominance of later arrivals, have been observed in alpine and forest communities. However, the potential for evolutionary priority effects to persist in an era of rapid global change remains unclear.
- Here, we use a natural experiment of historical disturbance in New Zealand to test whether anthropogenic changes in available habitat and nonnative invasion eliminate the role of evolutionary priority effects in community assembly. We also test whether evolutionary priority effects diminish with decreasing resource availability.
- Older plant clades, as estimated by clade crown age, were relatively more abundant in both primary and secondary grassland. Relative abundance in primary grassland decreased with clade stem age, but only weakly. However, for both clade age estimates, relative abundance decreased with age when nonnative biomass was high and soil moisture was low.
- Our data show that patterns in community structure consistent with evolutionary priority effects can occur in both primary and secondary grasslands, the latter created by anthropogenic disturbance. However, nonnative invasion may overwhelm the effect of immigration timing on community dominance, possibly as a result of high immigration rates and preadaptation to anthropogenically modified environments.

Introduction

The order and timing of arrival of ancestral taxa into new habitats can shape extant community structure via an evolutionary priority effect (Fukami, 2015). This effect is comparable to an ecological priority effect, where early-arriving colonizers are advantaged in a local community (Körner *et al.*, 2008; Fukami *et al.*, 2010; von Gillhaussen *et al.*, 2014). For evolutionary priority effects, early-arriving lineages exploit the ecological opportunity available when encountering a new habitat by having adequate time to adapt (De Meester *et al.*, 2016), spread and diversify (Fukami *et al.*, 2007), whereby the resulting clade occupies a broader niche than the ancestral colonist (Silvertown *et al.*, 2005; Tanentzap *et al.*, 2015). The expanded ecological ranges of clades with early-arriving ancestors may result from multiple processes, such as reduced interspecific interactions in the new habitat (Tingley *et al.*, 2014) and increasing phenotypic variability that broadens the niche (Van Valen, 1965). Wide-ranging taxa with large populations may subsequently diversify further, particularly during cycles of climate-driven population isolation and expansion (Wilson, 1959; Winkworth *et al.*, 2005). By exploiting ecological opportunities, early-arriving lineages may thus preempt niche space (sensu Fukami, 2015) and preclude establishment and dominance of later arrivals (Silvertown, 2004; Silvertown *et al.*, 2005; Tanentzap *et al.*, 2015). We have observed evidence for this pattern in alpine and forest plant communities in New Zealand (Lee *et al.*, 2012; Leopold *et al.*, 2015; Tanentzap *et al.*, 2015; Brandt *et al.*, 2016).

Despite their importance for extant communities, the potential for evolutionary priority effects to endure through an era of rapid global change remains an open question. If early-arriving lineages have broader niches and can thus monopolize newly created niche space, such as open alpine habitat created by mountain uplift (Lee *et al.*, 2012; Tanentzap *et al.*, 2015), can they expand into and dominate in comparable new habitat created by anthropogenic disturbance? The mechanism for monopolization via evolutionary priority effects first involves lineage diversification, which subsequently facilitates niche preemption of later arrivals by enhancing competitive ability (Silvertown, 2004; Silvertown *et al.*, 2005; Tanentzap *et al.*, 2015). Habitat conversion through anthropogenic activities may be too rapid and recent for the evolution of new taxa. Therefore, we might expect the strength of evolutionary priority effects to diminish in secondary habitat, depending also on the degree of similarity with the original eco-evolutionary context.

Here we test whether the strength of evolutionary priority effects differs in primary vs secondary grassland of New Zealand using a natural experiment of historical anthropogenic disturbance, which created new habitat (i.e. niche space) suitable for grassland clades to fill. Before human settlement, most of New Zealand's low-elevation area was forested and grasslands were largely restricted to the alpine zone, frosted valley basins and wetland bogs (Ausseil *et al.*, 2011; Heenan & McGlone, 2013). Following Polynesian (13th century) and, later, European settlement (19th century), much of the lowland and montane forest east of the South Island Alps was cleared, primarily via burning (McWethy *et al.*, 2010). Anthropogenic disturbance has thus dramatically increased the extent of lowland and montane indigenous grasslands in New Zealand in the recent past (Ausseil *et al.*, 2011). Given the extent and location of deforestation, environmental differences between primary and secondary grassland in New Zealand are likely to be particularly strong (Perry *et al.*, 2012). Thus, patterns of community structure consistent with evolutionary priority effects (i.e. dominance of early- as opposed to later-arriving clades in New Zealand) in both grassland types would provide evidence that past evolutionary processes play an enduring role in community assembly irrespective of major disturbance and the availability of new habitat.

We also test whether evolutionary priority effects weaken in communities invaded by nonnative species. We hypothesize that nonnative invasion reduces the role of evolutionary priority effects in community assembly via two mechanisms, increased immigration rate and selective preadaptation of species to anthropogenically modified ecosystems. On the first mechanism, theory suggests that immigration rates must be low relative to local community dynamics for priority effects to occur (Fukami, 2015). The rate of human-assisted colonization and establishment in New Zealand is much greater (multiple species per decade) than unassisted colonization and *in situ* diversification rates (multiple species over millions of yr). Colonization rates before the 19th century would have been low as New Zealand was isolated from potential source populations by at least 1000 km (Lee *et al.*, 2016). European settlement massively increased the immigration rate of plant species to New Zealand, approximately doubling the species richness of the vascular flora within two centuries (Williams & Cameron, 2006). Unlike natural immigration, these recent human-assisted introductions to New Zealand have arrived too recently to diversify and preempt niche space of later arrivals. As such, dominance hierarchies in communities invaded by nonnative species are unlikely to be associated with lineage arrival times across evolutionary timescales. As for the second mechanism, it is thought that strong evolutionary priority effects may occur only when immigrants are marginally adapted to local conditions. When immigrants are well adapted to the new environment, they would not require the advantage of early arrival to dominate the community and may be less likely to diversify as a result of, for example, difficulty in shifting between multiple adaptive peaks or competitive suppression of descendants with mutations (Knope *et al.*, 2012; Fukami, 2015; Tanentzap *et al.*, 2015).

Finally, we test how soil resource gradients (moisture and fertility) in primary and secondary grasslands influence the strength of evolutionary priority effects. Anthropogenic deforestation expanded the environmental range of indigenous grasslands in New Zealand, particularly into warm, dry and lowland areas (Ausseil *et al.*, 2011; Perry *et al.*, 2012). We have previously demonstrated that the strength of evolutionary priority effects attenuates along environmental stress gradients (Leopold *et al.*, 2015; Brandt *et al.*, 2016), consistent with the stress gradient hypothesis about the role of competition in community assembly (Bertness & Callaway, 1994). These findings highlight that priority effects are strongest in benign or resource-rich environments (Kardol *et al.*, 2013; Vannette & Fukami, 2014). Here we test whether the influence of environmental conditions on evolutionary priority are consistent in primary grasslands above the historic treeline vs human-modified landscapes (i.e. secondary grasslands where forest was cleared). Because precipitation tends to increase with elevation (Wratt *et al.*, 2000; Sundqvist *et al.*, 2013), moisture stress may be a stronger driver of community assembly in secondary than in primary grasslands. By contrast, soil fertility often decreases with elevation (Sundqvist *et al.*, 2013), and so may be more limiting in primary grasslands.

We use primary and secondary grassland community data from Mt Cardrona, South Island, New Zealand, to address whether evolutionary priority effects persist following anthropogenic habitat conversion and attenuate with both nonnative plant species invasion and decreasing resource availability. We approximate immigration timing of native grassland lineages as divergence of New Zealand clades from their nearest relatives overseas within dated phylogenies (following Winkworth *et al.*, 2005; Gehrke & Linder, 2011; Cornuault *et al.*, 2013; Hennequin *et al.*, 2014). We hypothesize that evolutionary priority effects will be consistent across primary and secondary grasslands (i.e. no difference in the effect of plant clade age on relative abundance above vs below the estimated historic treeline); that the effect of plant clade age will diminish with increasing nonnative invasion, as increased immigration and novel traits confound evolutionary effects of native plant species; and that the effect of plant clade age will diminish with decreasing soil resources in accordance with the stress gradient hypothesis, with different soil resources driving this interaction in primary vs secondary grasslands.

Materials and Methods

Abiotic and biotic sampling

We used grassland vegetation data that were collected in a nested sampling design along the ridgeline of Mt Cardrona, South Island, New Zealand (44°51′S, 168°57′E), for a comprehensive study of altitudinal gradients (Mannall, 2014; McCann, 2015; Wu *et al.*, 2017). To obtain a more representative sample of the grassland communities, we sampled both the north- and south-facing slopes of the mountain's ridgeline because plant community composition can be as variable across the ridgeline at the same altitude as between different altitudes. For example, shrubs are often restricted to the south-facing slope (low irradiation), while grasses are more abundant on the north-facing slope (drier, more irradiated; B. J. Anderson, pers. obs.). Sixteen transects perpendicular to the ridgeline were located at *c.* 100 m altitudinal intervals from the valley floor (495 m above sea level (asl)) to just below the summit (1900 m asl), with two transects at either end of a plateau at 1300 m asl. Five clusters of five 20 × 20 cm plots were evenly spaced along each transect, with two clusters on the southern aspect, one on the ridgeline, and two on the northern aspect (see Supporting Information Fig. S1 for a diagram of the sampling design). An additional plot cluster was located on the mountain summit (1936 m asl); thus a total of 405 plots were sampled. Plots were sized to closely relate vegetation to soils data. Above-ground biomass was clipped from all vegetation in each plot in summer (27–31 January 2014), sorted to plant species, dried to constant mass at 60°C, and weighed. Species richness per plot ranged from 1 to 18 and total live vascular plant biomass ranged from 0.08 to 412 g, with the most common species (*Anthoxanthum odoratum*) occurring in 55% of plots (see Fig. S2 for species and biomass accumulation curves in relation to sampling effort). A soil core (4 cm diameter, 10 cm depth) was taken in the centre of each plot to measure gravimetric soil moisture (samples weighed before and after drying for 96 h at 105°C) and chemistry (Environmental Chemistry Laboratory, Landcare Research, Palmerston North, New Zealand). Soil chemistry was determined as pH in water at a 1 : 2.5 ratio, total organic carbon (C) and total nitrogen (N) measured via combustion using a Leco TruMac (St Joseph, MI, USA), available ammonium (NH_4^+) and nitrate (NO_3^-) using KCl extraction, and available phosphorus (P) following the Olsen method using sodium bicarbonate extraction.

Estimating immigration timing

We estimated immigration timing for the 24 plant clades in our dataset for which published dated molecular phylogenies were available (hereafter, 'focal clades'; Table 1). Ages were 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). Where data existed, we also considered the age of the New Zealand clade's most recent common ancestor (i.e. crown age). Because each of these clades originated long after New Zealand was isolated from other Gondwanan landmasses (i.e. New Zealand separated from Australia and Antarctica > 80 million yr ago), biogeographical analyses suggest that their ancestors colonized New Zealand from overseas following long-distance dispersal (Smissen *et al.*, 2003; Meudt & Simpson, 2006; Himmelreich *et al.*, 2012; Birch *et al.*, 2014; Cantley *et al.*, 2016). We deferred to the cited sources for identification of clades hypothesized to have radiated within New Zealand, and most of our focal taxa have been well sampled in New Zealand and global phylogenies for both systematics and biogeographical analyses (Table 1). It is possible that stem ages overestimate the timing of immigration to New Zealand, such as via extinction of or lack of inclusion in the phylogeny of a nearer overseas relative than the contemporary taxa sampled (Gehrke & Linder, 2011; Everson *et al.*, 2016). By contrast, crown ages may underestimate the timing of immigration, such as if radiation within New Zealand occurred following a lag after colonization (Pirie *et al.*, 2010; Gehrke & Linder, 2011). Nonetheless, stem and crown age estimates were closely correlated in the 14 clades for which both were available ($r = 0.95$, $P < 0.0001$ from a one-tailed test on log-transformed ages), indicating that the arrival order of focal clades is likely to change little regardless of which age is used to estimate immigration timing.

There is also no 'true' estimate of a node age, and values will be partly influenced by the assumptions and methods used in constructing and dating underlying phylogenies (Sauquet *et al.*, 2012). Therefore, we used a distribution of potential ages in our analyses to explicitly incorporate the variance around each mean age into our statistical model. We estimated a variance for each clade age using the standard deviation (SD) or the longer of the two tails of the 95% highest posterior density interval of the reported stem age estimate (sensu Lee *et al.*, 2012; Leopold *et al.*, 2015; Tanentzap *et al.*, 2015; Brandt *et al.*, 2016). We test our hypotheses using a separate analysis for stem and crown ages of each focal clade to examine the broadest possible suite of focal clades. The 19 focal clades with a reported stem age were present in 357 plots in the dataset and the 19 focal clades with a reported crown age were present in 358 plots, and thus only these plots were included in each of the analyses. The 32 species in focal clades with corresponding stem ages represented 24% of the species present (35% of the native species) in all 405 plots sampled and 75% of the total vascular biomass collected (86% of the native biomass); the 31 species in the focal clades with corresponding crown ages represented 23% of the total species (34% of the native species) and 70% of the total biomass (81% of the native biomass).

Statistical analyses

We used the field plot data to derive indices of community dominance and soil fertility. We calculated relative abundance A_{ijkl} of each focal plant clade i by summing the live vascular plant biomass of all species in the clade and dividing by the total live biomass in plot j of plot cluster k on elevation transect l. We estimated clade richness on Mt Cardrona ('site clade diversity' s_i) as the total number of species within each clade observed in our dataset and used published floras to obtain the maximum height h_i of those clades (Table 1). We estimated a soil fertility index for plots containing focal clades f_{jkl} as the first axis of a principal components analysis (PCA) on soil pH, organic C, total N, C : N (calculated from organic C and total N), NH_4^+, NO_3^- and P, all centred and scaled, using the LABDSV library (Roberts, 2007) in R v.3.2.2 (R Core Team, 2015). The PCA axis explained 44% of the variance in soil chemistry for both subsets of plots (i.e. used in stem age and crown age analysis) and was positively correlated with organic C ($r = 0.51$ in both cases), total N ($r = 0.52$ in both cases), NH_4^+ ($r = 0.44$ in both cases), NO_3^- ($r = 0.38$–0.39) and P ($r = 0.31$–0.32), and negatively correlated with pH ($r = -0.14$ in both cases).

We fitted a linear mixed model to test our hypotheses about evolutionary priority effects in primary and secondary grasslands. To determine whether evolutionary priority effects occur following anthropogenic habitat conversion, we compared the strength

Table 1 Immigration timing, phylogenetic coverage of dated phylogeny, diversity, plot occupancy and stature of 24 focal clades observed in grassland plots at Mt Cardrona, New Zealand

Clade, with generic or tribal naming authority	Stem age (Myr)	Crown age (Myr)	Sister taxa used for age estimation	Percentage of NZ species included	Percentage of species in genus/tribe included	Age references	Site clade diversity	No. occurrences	Maximum height (m)
Abrotanella (Gaudich.) Cass.*†	6.60 (10.10–4.30)	3.80 (5.70–2.20)	South American *Abrotanella* clade	100% (10 of 10)	95% (20 of 21)	Swenson *et al.* (2012)	1	3	0.1‡
Aciphylleae M.F. Watson & S.R. Downie	34.80 (48.20–22.30)	11.00 (17.60–5.70)	Sino-Himalayan *Acronema* clade	11% (8 of 70)§	11% (8 of 72)	Spalik *et al.* (2010)	4	32	1
Chaerophyllum L.	1.60 (2.60–0.80)	0.60 (1.10–0.20)	Australasian-American 'Oreomyrrhis' clade of *Chaerophyllum*	100% (4 of 4)	52% (34 of 65)	Spalik *et al.* (2010)	1	41	0.3
Chionochloa Zotov†	19.95 (23.60–16.65)¶	8.60 (13.95–4.50)¶	South American *Cortaderia* clade	96% (22 of 23)	92% (23 of 25)	Antonelli *et al.* (2010); Pirie *et al.* (2012)	2	167	1.5‡
Coprosma J. R.Forst. & G.Forst.†	25.48 (30.50–23.10)	13.73 (18.40–9.10)	Circum-Pacific *Nertera* clade	88% (52 of 59)	93% (102 of *c.* 110)	Cantley *et al.* (2016)	2	5	0.05‡
Craspedia G.Forst.	3.10 ± 0.60¶	Not reported	Australian *Craspedia alba* clade	71% (5 of 7)§	83% (20 of 24)	Ford *et al.* (2007); K. A. Ford, pers. comm. (2011)	1	2	0.1‡
Dracophyllum Labill.	7.40 (11.20–6.90)	6.10 (6.30–2.30)	New Caledonian *Dracophyllum* – Australian *Richea acerosa* clade	51% (19 of 37)§	73% (35 of 48)	Wagstaff *et al.* (2010)	2	55	0.05
Festuca L.*	8.90 ± 1.70	5.30 ± 1.70	North American *Festuca californica*	90% (9 of 10)	39% (176 of *c.* 450)	Inda *et al.* (2008)	1	153	1‡
Gaultheria Kalm ex L.†	14.46 (22.40–6.89)	7.74 (14.03–2.09)	South American *Gaultheria myrsinoides*	10% (1 of 10)§	29% (39 of 134)	Schwery *et al.* (2015)	2	47	0.1
Hydrocotyle L.	8.33 (14.40–3.00)	Unavailable	Southeast Asian *Hydrocotyle sibthorpioides*	10% (1 of 10)§	3% (5 of *c.* 200)	Nicolas & Plunkett (2014)	1	49	0.05‡
Leptinella Cass.†	Error estimates not reported	10.30 (14.10–6.60)	Australian/New Guinean *Cotula* – *Leptinella* clade	100% (25 of 25)	94% (32 of 34)	Himmelreich *et al.* (2012)	2	23	0.05‡
Myosotis L.†	2.85 (3.42–2.00)	1.87 (2.24–0.91)	Spanish *Myosotis persoonii*	81% (34 of 42)	59% (59 of *c.* 100)	Meudt *et al.* (2015a)	2	4	0.03
Ophioglossum L.†	11.51 (20.82–4.24)	6.33 (12.35–1.57)	Geographically widespread *Ophioglossum pusillum* clade	100% (2 of 2)	27% (8 of 30)	Papadopulos *et al.* (2011); A. S. T. Papadopulos, pers. comm. (2015)	1	1	0.76‡
Ourisia Comm. ex Juss.	Not reported	0.80 (1.30–0.40)	Tasmanian *Ourisia integrifolia*	93% (13 of 14)§	50% (14 of 28)	Meudt *et al.* (2009)	1	1	0.135‡
Plantago L.†	1.62 ± 0.40¶	Not reported	*Plantago major*	91% (10 of 11)	10% (27 of *c.* 270)	Tay *et al.* (2010)	1	2	0.02‡
Poa L. (Brizoides)*†	3.20 (4.85–1.75)¶	2.35 (3.65–1.15)¶	Australian *Poa* section Brizoides clades A and B	31% (12 of 39)§	14% (70 of *c.* 500)	Birch *et al.* (2014)	1	57	0.7‡
Poa L. (X clade)*†	3.55 (5.50–1.80)¶	Not reported	Eurasian *Poa arctica* – Russian *Poa smirnowii*	31% (12 of 39)§	14% (70 of *c.* 500)	Birch *et al.* (2014)	3	152	0.4‡
Rytidosperma Steud. (*R. australe* clade)*	3.85 (5.55–2.35)¶	3.10 (4.55–1.75)¶	Chilean *Rytidosperma* clade	67% (14 of 21)§	78% (57 of 73)	Antonelli *et al.* (2010); Pirie *et al.* (2012)	1	4	0.5‡
Rytidosperma Steud. (*R. buchananii* clade)*	Error estimates not reported	2.00 (3.45–0.85)¶	Australian *Rytidosperma* clade	67% (14 of 21)§	78% (57 of 73)	Antonelli *et al.* (2010); Pirie *et al.* (2012)	2	90	0.45‡
Rytidosperma Steud. (*R. clavatum* clade)*†	2.85 (3.90–1.90)¶	1.90 (3.10–0.95)¶	Australian/Chilean *Rytidosperma caespitosum* clade	67% (14 of 21)§	78% (57 of 73)	Antonelli *et al.* (2010); Pirie *et al.* (2012)	1	52	0.9‡
Scleranthus L.†	2.48 ± 0.57	Not reported	Australian *Scleranthus fasciculatus*	100% (3 of 3)	100% (10 of 10)	Smissen *et al.* (2003)	2	11	0.05‡
Veronica L.	10.21 (13.33–7.21)	7.62 (10.26–5.29)	Australian *Veronica* section Labiatoides	40% (51 of 127)§	28% (128 of *c.* 450)	Meudt *et al.* (2015b)	3	14	0.2
Wahlenbergia Schrad. ex Roth (NZ clade 1)*	Error estimates not reported	0.70 (1.29–0.15)	Australian *Wahlenbergia* clade	100% (11 of 11)	21% (54 of 260)	Prebble *et al.* (2011)	1	1	0.5‡

Table 1 (Continued)

Clade, with generic or tribal naming authority	Stem age (Myr)	Crown age (Myr)	Sister taxa used for age estimation	Percentage of NZ species included	Percentage of species in genus/ tribe included	Age references	Site clade diversity	No. occurrences	Maximum height (m)
Wahlenbergia Schrad. ex Roth (NZ clade 2)*	Error estimates not reported	1.60 (2.78–0.55)	Australian *Wahlenbergia gracilis*	100% (11 of 11)	21% (54 of 260)	Prebble *et al.* (2011)	1	150	0.25

Stem and crown ages (millions of yr (Myr)), with uncertainty estimates of ± SD or 95% highest posterior density interval as provided by the listed references, provide a proxy for immigration timing of the focal clades. Stem age represents the age of divergence of the clade from its nearest relative outside New Zealand ('Sister taxa') in phylogenies that include the listed percentage of New Zealand and global species in each genus or tribe. Crown age represents the age of the clade's most recent common ancestor. Site clade diversity is the total number of species in each focal clade observed across all 405 sampled plots at Mt Cardrona; number of occurrences is the number of plots in which a clade was observed; and maximum clade height is the maximum height of the observed species in each clade from published floras (Allan, 1961, unless otherwise indicated).

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

†Clade in the cited phylogeny includes Australasian species outside New Zealand, but phylogenetic and biogeographical analysis suggests New Zealand is the ancestral origin for all clades except *Plantago*, *Poa* and *Scleranthus*.

‡Maximum clade height estimated as culm length (*Chionochloa*, *Festuca*, *Poa*, *Rytidosperma*; Edgar & Connor, 2010), frond length (*Ophioglossum*), and for prostrate and rosette growth forms (*Abrotanella*, *Craspedia*, *Hydrocotyle*, *Leptinella*, *Plantago*). Additional references used for *Coprosma* (Orchard, 1987), *Ourisia* (Meudt, 2006), *Scleranthus* (Webb *et al.*, 1988) and *Wahlenbergia* (Petterson, 1997).

§More complete taxon sampling for these genera/tribes supports monophyly of these focal clades in New Zealand or Australasia and identity of the listed sister taxa: Aciphylleae (37 species, with ancestral origin in New Zealand; Banasiak *et al.*, 2013), *Gaultheria* (13 of 14 Australasian species, with New Zealand as ancestral origin; Bush *et al.*, 2009) and *Ourisia* (26 species; Meudt & Simpson, 2006). Additional evidence for radiation within New Zealand in less well-sampled clades is the proportion of New Zealand species that are endemic: 100% of Aciphylleae, *Craspedia*, *Dracophyllum* and *Ourisia*, 95% of *Poa*, 92% of *Veronica*, 90% of *Gaultheria* and *Hydrocotyle*, and 86% of *Rytidosperma* (Plant Names Database; http://nzflora.landcareresearch.co.nz/).

¶Reported stem age and uncertainty were averaged from multiple estimates within and/or among listed references.

of the relationship between relative abundance A_{ijkl} and plant clade age t_i above and below the estimated historic treeline at Mt Cardrona (i.e. in primary vs secondary grassland, respectively; elevation group g). We estimated historic treeline at 1150 m asl according to extant treelines at a similar latitude in New Zealand (Cieraad & McGlone, 2014; Leopold *et al.*, 2015; Brandt *et al.*, 2016). Charcoal data paired with pollen records for sites near Mt Cardrona suggest that deforestation by fire was significant in the immediate region following initial human arrival to New Zealand (McWethy *et al.*, 2010). Furthermore, modelling shows a high probability of forest loss in the vicinity of Mt Cardrona (i.e. in between Lakes Wakatipu and Wanaka; Perry *et al.*, 2012). To determine whether evolutionary priority effects diminished with nonnative invasion, we tested whether the effect of clade age t_i decreased with nonnative plant biomass c_{jkl} (i.e. $t_i \times c_{jkl}$ interaction), with separate effects estimated above vs below the historic treeline (i.e. for each elevation group g). We used nonnative biomass rather than proportion abundance to estimate invasion to avoid circularity in estimating the effect of relative abundance of nonnatives on relative abundance of focal clades. To determine whether evolutionary priority effects diminished with decreasing resource availability, we similarly tested whether the effect of clade age t_i increased with both soil moisture m_{jkl} and fertility f_{jkl} (i.e. $t_i \times$ soil resource interaction), with separate effects estimated above vs below the historic treeline (i.e. for each elevation group g). We included site clade diversity s_i as a predictor in our model to control for the possibility that species from more diverse clades may co-occur more frequently or with greater abundance than species from less diverse clades simply because of greater diversity. We also included maximum clade height h_i as a predictor to allow for clades to differ in relative abundance as a result of differences in individual plant size. We did not expect the effect of site clade diversity or height to differ above vs below the historic treeline. To predict the logit transformation of A_{ijkl}, which accounted for the fact that proportions are bounded between 0 and 1 and produce nonnormal errors, our model took the form:

$$\mathrm{logit}(A_{ijkl}) \sim N(\mu_{ijkl}, \sigma_i),$$

$$\begin{aligned}\mu_{ijkl} = {} & \alpha_g + \beta_g^{(1)} \log_e(t_i) + \beta_g^{(2)} c_{jkl} + \beta_g^{(3)} m_{jkl} + \beta_g^{(4)} f_{jkl} \\ & + \beta_g^{(5)} \log_e(t_i) c_{jkl} + \beta_g^{(6)} \log_e(t_i) m_{jkl} + \beta_g^{(7)} \log_e(t_i) f_{jkl} \\ & + \gamma s_i + \eta h_i + \varepsilon_{jkl} + \varepsilon_{kl} + \varepsilon_l,\end{aligned}$$

where α_g is the mean relative abundance across all clades within elevation group g (i.e. above vs below the historic treeline), $\beta_g^{(1)}$ is the effect of clade age t_i, $\beta_g^{(2)}$ is the effect of nonnative biomass c_{jkl}, $\beta_g^{(3)}$ is the effect of soil moisture m_{jkl}, $\beta_g^{(4)}$ is the effect of soil fertility f_{jkl}, $\beta_g^{(5)}$, $\beta_g^{(6)}$ and $\beta_g^{(7)}$ are the changes in the effect of clade age with increasing nonnative biomass, soil moisture and soil fertility, respectively, γ is the effect of site clade diversity s_i, and η is the effect of maximum clade height h_i. We included variation among plots ε_{jkl}, plot clusters ε_{kl} and elevation transects ε_l to account for the fact that relative abundances of clades in the same plot, among plots in the same cluster, and among plots on the same transect were nonindependent. Because five plots contained only *Chionochloa* spp., we added $(1 - A_{\max})$ to both the numerator and denominator of the logit transformation, where $A_{\max}$ was the maximum proportion of plot biomass across all plots that was < 1 (Warton & Hui, 2011). We propagated uncertainty associated with mean published estimates of t_i into the model as $\sigma_i = \sqrt{(\tau_i(\beta_g^{(1)} + \beta_g^{(5)} c_{jkl} + \beta_g^{(6)} m_{jkl} + \beta_g^{(7)} f_{jkl})/t_i)^2 + \sigma^2}$, where τ_i and σ are the observed SD for each clade i derived from published studies and an estimated residual SD, respectively. We used the same model to examine the effects of stem age and crown age as metrics of clade age.

We fitted our model within a Bayesian framework by calling Stan via RStan 2.7.0 (Stan Development Team, 2015). We assigned uninformative priors for model parameters: $\sim N(0, 100)$ for regression coefficients and $\sim U(0, 40)$ for SD. We standardized all predictors to a mean of 0 and SD of 1 so that estimated effects represented a change in relative abundance with 1 SD change in the predictor. We simulated three Markov chain Monte Carlo (MCMC) chains of 9000 or 7000 iterations with a burn-in of 4000 or 3000 runs and thinning of 10 or 8 for stem or crown age models, respectively. 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 that all main parameters had an effective sample size > 700 (Gelman & Hill, 2007). A posterior predictive check showed the models fitted the data well (Bayes $P = 0.52$ and 0.48 for the model using stem age and crown age, respectively, or nearly half of the model iterations reported sums of squared residuals greater than those from simulated data drawn from the modelled distribution), and both models explained approximately one-quarter to one-third of the variance in the data (Bayesian $R^2 = 0.22$ and 0.34 for the stem and crown age model, respectively).

We calculated posterior means and 95% credible intervals (CIs) from the combined net output of all three MCMC chains to infer model parameter effects. We used three predictions to test our hypotheses. First, if priority effects are consistent across primary and secondary grassland, we expected no difference in the effect of clade age on relative abundance above vs below the historic treeline (i.e. 95% CI of the difference between $\beta_1^{(1)}$ and $\beta_2^{(1)}$ overlaps zero). Second, if nonnative invasion weakens the role of priority effects, we expected a negative interaction between clade age and nonnative biomass $\beta^{(5)}$. Third, if priority effects diminish with decreasing resource availability, we expected a positive interaction between clade age and soil moisture $\beta^{(6)}$ and between clade age and soil fertility $\beta^{(7)}$.

Results

Model using stem age

On average, relative abundance within plots weakly decreased with stem age above the estimated historic treeline (Fig. 1a) and was unaffected by stem age below the treeline (Table 2; Fig. 1e). Above the historic treeline, relative abundance decreased with stem age most strongly in plots with high nonnative biomass and low soil moisture (Table 2; Fig. 1b,c). However, as predicted, the effect of stem age at the average levels of invasion and soil resource availability did not differ between primary and secondary grasslands ($\beta_1^{(1)} - \beta_2^{(1)} = -0.45$, 95% CI: -1.16–0.22). Across all grasslands, clade diversity at Mt Cardrona did not affect relative abundance, but clades of larger stature were more dominant (Table 2).

Relative abundance above the historic treeline decreased with stem age when nonnative biomass was high (highest four quantiles; Fig. 1b; Table 2), but no significant effect was detected below the treeline (Fig. 1f). This difference was not a result of greater invasion above than below the treeline. Nonnative plant biomass averaged 1.34 ± 0.10 g (mean ± SE) per plot above the historic treeline and 7.06 ± 0.43 g below the historic treeline ($8.1 \pm 0.7\%$ and $47.2 \pm 2.2\%$ of total plot biomass, respectively; Fig. 2a).

Above the historic treeline, the stem age effect changed from neutral at high soil moisture to negative at low soil moisture (Table 2; Fig. 1c). However, stem age did not interact with soil moisture to affect relative abundance below the historic treeline and did not interact with soil fertility anywhere (Table 2; Fig. 1d, g,h). Soil moisture was higher, on average, above the historic treeline ($32.8 \pm 0.4\%$) than below ($17.1 \pm 0.6\%$; Fig. 2b), but the soil fertility index did not differ, on average, above the historic treeline (0.05 ± 0.05) from the value below (-0.09 ± 0.14) the historic treeline (Fig. 2c; see Fig. S3 for elevation trends in each soil chemistry variable).

The effects of stem age on relative abundance were robust to including only the 11 clades that were observed both above and below the historic treeline (Table S1; Fig. S4). However, the stem age effect was more negative above than below the historic treeline when this subset of clades was analysed ($\beta_1^{(1)} - \beta_2^{(1)} = -0.86$, 95% CI: -1.68 to -0.02).

Model using crown age

Relative abundance within plots increased with crown age both above and below the estimated historic treeline (Table 2; Fig. 3). As predicted, the effect of crown age did not differ between primary and secondary grasslands ($\beta_1^{(1)} - \beta_2^{(1)} = -0.16$, 95% CI: -0.70–0.31). Unexpectedly, relative abundance decreased with clade diversity at Mt Cardrona (Table 2). Across all grasslands, relative abundance increased with the clade's stature (Table 2).

Above the historic treeline, the positive relationship between crown age and relative abundance diminished (and was eventually reversed to become negative) with increasing nonnative biomass (Table 2; Fig. 3b). Below the treeline, no interactive effect of nonnative biomass was observed (Table 2; Fig. 3f). The crown age effect on relative abundance above the historic treeline changed from positive at the lowest quantile of nonnative biomass to negative at the highest two quantiles (Fig. 3b). As with the stem age model, this interaction was not a result of greater invasion above than below the treeline (Fig. S5).

As predicted, evolutionary priority effects diminished with decreasing resource availability above the historic treeline (Table 2), where the crown age effect changed from positive at

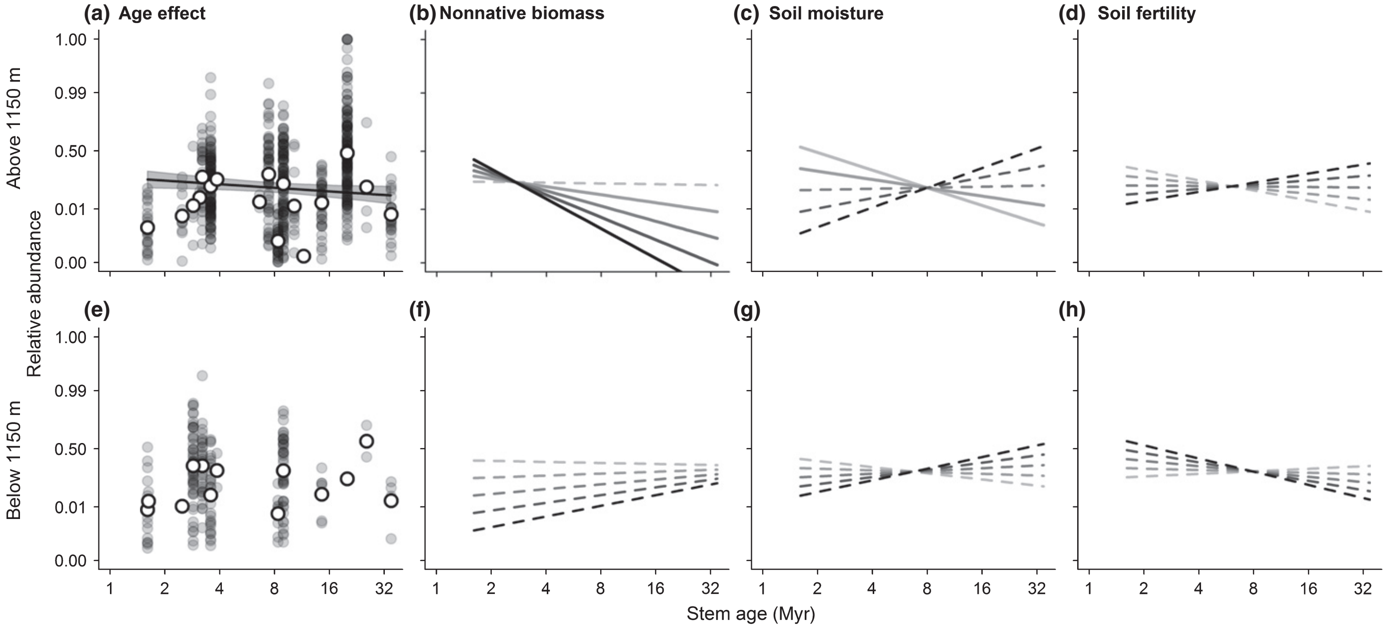

Fig. 1 Relative clade abundance in relation to stem age and its interactions with environmental variables above (a–d) and below (e–h) the estimated historic treeline on Mt Cardrona. (a, e) Light grey circles are responses for each focal plant clade in each plot ($n = 646$ above and 200 below); and white circles are clade means ($n = 17$ above and 13 below). Solid lines indicate mean relationships, with 95% credible intervals (CI) indicated by grey polygons. Interaction plots show predicted mean relationships between relative abundance and clade age at five intervals (light grey to black) of increasing: (b, f) nonnative biomass (0–13.9 g above and 0–36.0 g below); (c, g) soil moisture (8.02–73.92% above and 1.43–38.99% below); (d, h) soil fertility index (−2.33–4.66 above and −1.96–21.08 below). Solid lines indicate a nonzero slope; dashed lines indicate that the 95% CI for the slope overlaps zero. Trendlines derived from 1500 posterior samples of the model. Myr, millions of yr.

high soil moisture to neutral at low soil moisture (Fig. 3c). However, crown age did not interact with soil moisture to affect relative abundance below the historic treeline and did not interact with soil fertility anywhere (Table 2; Fig. 3d,g,h; see Figs S5 and S6 for elevation trends in soil resources).

The effects of crown age on relative abundance were largely robust to including only the 11 clades that were observed both above and below the historic treeline (Table S1; Fig. S7). Moreover, the effect of crown age on relative abundance above the historic treeline changed from positive at high soil fertility to neutral at low soil fertility, providing further support to our prediction that evolutionary priority effects diminish with decreasing resource availability (Fig. S7d).

Discussion

Our data show that relative abundance of plant clades increases with crown age in communities both above and below the historic treeline at Mt Cardrona, while relative abundance above the historic treeline decreases with stem age. The effect of clade age in both models with 19 clades did not differ between primary and secondary grassland (i.e. above vs below the historic treeline). Our results thus provide some support for our hypothesis that evolutionary priority effects occur even in secondary grassland, or anthropogenically created habitat. However, the different trends we observed using stem age vs crown age as proxies for immigration timing demonstrate that

Table 2 Mean parameter estimates with 95% credible intervals (CIs) for models of relative abundance of 24 focal plant clades (19 included in each model) in primary and secondary grassland at Mt Cardrona (i.e. above and below the historic treeline (1150 m above sea level (asl)), respectively)

	Relative abundance in stem age model		Relative abundance in crown age model	
	Above treeline	Below treeline	Above treeline	Below treeline
Intercept (α)	**−2.04 (−2.84 to −1.22)**	**−2.06 (−3.80 to −0.30)**	**−4.53 (−5.13 to −3.92)**	**−3.30 (−4.58 to −2.00)**
Clade age ($\beta^{(1)}$)	**−0.33 (−0.63 to −0.02)**	0.12 (−0.51–0.76)	**0.74 (0.47–1.01)**	**0.90 (0.43–1.42)**
Nonnative biomass ($\beta^{(2)}$)	0.58 (−0.57–1.69)	**−1.03 (−1.83 to −0.35)**	**0.81 (0.16–1.51)**	**−0.67 (−1.10 to −0.24)**
Soil moisture ($\beta^{(3)}$)	**−1.33 (−2.61 to −0.11)**	−0.92 (−2.17–0.24)	**−0.90 (−1.61 to −0.22)**	−0.45 (−1.31–0.42)
Soil fertility ($\beta^{(4)}$)	−0.69 (−1.90–0.57)	0.31 (−0.23–1.01)	−0.31 (−1.02–0.40)	0.18 (−0.15–0.50)
Clade age × nonnative biomass ($\beta^{(5)}$)	**−0.47 (−0.90 to −0.05)**	0.18 (−0.13–0.54)	**−0.72 (−1.04 to −0.40)**	−0.13 (−0.43–0.20)
Clade age × soil moisture ($\beta^{(6)}$)	**0.52 (0.09–0.97)**	0.40 (−0.13–0.97)	**0.42 (0.12–0.76)**	0.12 (−0.29–0.56)
Clade age × soil fertility ($\beta^{(7)}$)	0.32 (−0.11–0.74)	−0.12 (−0.64–0.36)	0.24 (−0.08–0.56)	−0.13 (−0.49–0.18)
Site clade diversity (γ)	0.06 (−0.16–0.28)		**−0.47 (−0.67 to −0.25)**	
Maximum clade height (η)	**1.30 (1.07–1.54)**		**1.00 (0.78–1.22)**	

Values in bold have 95% CIs that exclude zero.

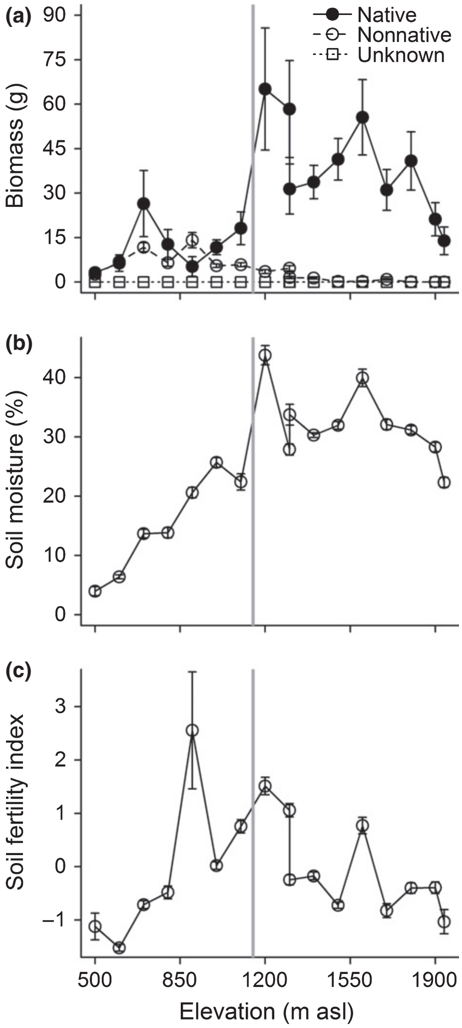

Fig. 2 Above-ground biomass by plant provenance (a), soil moisture (b) and soil fertility (c) in relation to elevation band sampled on the Mt Cardrona ridgeline (data are means ± SE of the 10–25 plots per elevation band that contained a focal clade for the stem age analysis, except at the summit of 1936 m above sea level (asl) where only five plots were sampled). The vertical grey line at 1150 m asl represents the estimated historic treeline; $n = 227$ plots above and 130 plots below. In (a), biomass of unknown provenance is from unidentified species or species identified to a genus that includes both native and nonnative species observed on Mt Cardrona. See Supporting Information Fig. S3 for similar trends in the subset of plots used in crown age analysis.

improved accuracy in estimating arrival order of plant lineages is essential to documenting patterns consistent with evolutionary priority effects. Although we did not observe a positive effect of stem age on relative abundance at Mt Cardrona, the effect sizes of crown age in both primary and secondary grasslands (Table 2) were similar to the effect size we observed in alpine communities in the Murchison Mountains (95% CI: 0.43–1.59, estimated using an identical modelling approach with stem age; Leopold *et al.*, 2015). Thus, our results suggest that evolutionary priority effects may operate in new niche space derived from anthropogenic habitat conversion (i.e. fire; McWethy *et al.*, 2010) and are robust to loss of some clades from the environment (Fig. S7). Moreover, this effect of clade age persists after controlling for differences in clade diversity and one proxy for clade fitness (i.e. height).

Early-arriving clades may be able to diversify and preempt niche space from later arrivals as a result of both encountering greater ecological opportunity upon arrival and having greater time to diversify (Tanentzap *et al.*, 2015). The older focal clades in our study were more diverse both at Mt Cardrona and throughout New Zealand (Fig. S8). However, the effects of clade age on diversity and relative abundance were independent. Relative abundance did not increase with clade diversity at Mt Cardrona; in particular, relative abundance decreased with clade diversity in the model using crown age (Table 2). Thus, our observation of a greater dominance of clades with older crown ages is unlikely to be solely the product of a time-to-diversify mechanism. Rather, older clades may be stronger competitors, possibly as a function of resource acquisition traits diverging early in radiations (Ackerly *et al.*, 2006), or have colonisation traits facilitating their expansion into new habitat as it becomes available, enabling them to outcompete young clades.

Many of the clades in our study arrived in New Zealand before the uplift of the Southern Alps (Heenan & McGlone, 2013) and were well positioned to expand into this newly created alpine habitat as it emerged. For example, widespread occupancy of lowlands by the snow tussock *Chionochloa* (Pirie *et al.*, 2010) and *Ranunculus* (Lockhart *et al.*, 2001) has facilitated diversification of alpine specialists in several subgeneric clades. Thus, although there is some regional differentiation in specific taxa across New Zealand, the same clades are involved throughout the primary grasslands. Evidence for delayed diversification in these lineages (e.g. difference between stem and crown age; Table 1) indicates that individual taxa from different clades may have simultaneously diverged and colonized local habitats created by mountain uplift. However, younger species in these clades may have remained dominant in local communities if they retained the ancestral phenotypes or genotypes that were advantageous when their founders originally arrived in New Zealand early in evolutionary time, such as enhanced competitive ability. Here we have shown that this evolutionary legacy tied to a clade's immigration timing can have similar consequences for community structure in new, analogous habitat created in the past few centuries.

We present the first evidence that nonnative invasion weakens evolutionary priority effects, whether immigration timing is estimated using clade stem age (Fig. 1b) or crown age (Fig. 3b). Human-assisted plant introductions could weaken evolutionary priority effects via the increased immigration rate of colonists relative to rates of *in situ* diversification of residents, and preadaptation of nonnative species to anthropogenically modified systems (Fukami, 2015). Furthermore, over short, ecological time, nonnative grassland species can exhibit stronger priority effects than those of natives, particularly when they exhibit functional differences such as earlier emergence (Wilsey *et al.*, 2015). Relative abundance of nonnative species in plots on Mt Cardrona was unrelated to their residence time in New Zealand, estimated using naturalisation dates in published floras (1844–1946; see Fig. S9). However, higher relative growth rates and nitrogen requirements of nonnative plant species compared with natives in

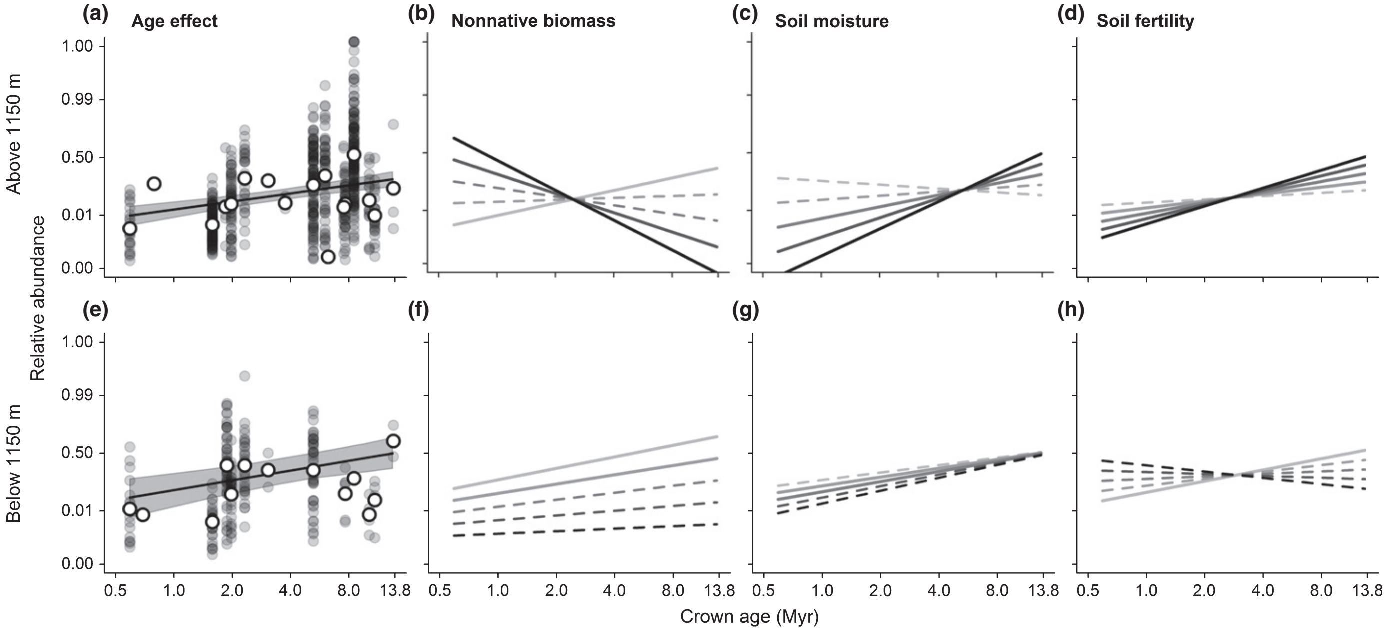

Fig. 3 Relative clade abundance in relation to crown age and its interactions with environmental variables above (a–d) and below (e–h) the estimated historic treeline on Mt Cardrona. (a, e) Light grey circles are responses for each focal plant clade in each plot ($n = 671$ above and 224 below); and white circles are clade means ($n = 17$ above and 13 below). Solid lines indicate mean relationships, with 95% credible intervals (CI) indicated by grey polygons. Interaction plots show the predicted mean relationships between relative abundance and clade age at five intervals (light grey to black) of increasing: (b, f) nonnative biomass (0–13.9 g above and 0–36.0 g below); (c, g) soil moisture (6.03–73.92% above and 1.43–38.99% below); and (d, h) soil fertility index (−2.29–4.61 above and −1.98–20.90). Solid lines indicate a nonzero slope; dashed lines indicate that the 95% CI for the slope overlaps zero. Trendlines derived from 1500 posterior samples of the model. Myr, millions of yr.

New Zealand grassland may enable them to exploit high resource conditions, for example, resulting in nonnative dominance in certain local communities regardless of arrival order (King & Wilson, 2006a,b; Gross *et al*., 2013). Thus, our findings suggest that invasion by species functionally different from the native community can overwhelm the advantage conferred by early arrival of ancestral taxa.

Nonnative plants can affect native species (Pyšek *et al*., 2012), but their effects do not always correlate with their abundance (Ricciardi *et al*., 2013). Here we demonstrate impacts of invasion on community assembly processes at a site where, on average, nonnative species remain less abundant than natives (nonnative plot biomass = 3.55 ± 0.28 g, native plot biomass = 30.73 ± 2.61 g (mean ± SE across 357 plots); Fig. 2a). In particular, although native species dominate communities above the historic treeline (Figs 2a, S5a), the role of evolutionary priority effects becomes more negative with increasing nonnative biomass in these habitats (Figs 1b, 3b). Different ecological processes may predominately govern assembly of native vs nonnative plant communities (e.g. Cadotte *et al*., 2010; but see Lemoine *et al*., 2015), and thus explain how the impact of invasion can be decoupled from nonnative species abundance. Such ecological differences may also affect the role of evolutionary priority effects on assembly.

In primary grassland (i.e. above the historic treeline), the effect of clade age diminished with decreasing soil moisture (Figs 1c, 3c). These results are consistent with our previous observations in alpine and forest communities, where evolutionary priority effects attenuated along environmental stress gradients (Leopold *et al*., 2015; Brandt *et al*., 2016). Similarly, other studies have shown the strength of ecological priority effects to increase with soil fertility (Ejrnæs *et al*., 2006; Kardol *et al*., 2013). Contrary to our predictions, evolutionary priority effects were not influenced by soil moisture or fertility in secondary grassland (i.e. below the historic treeline; Figs 1g,h, 3g,h). Thus, environmental conditions that mediate evolutionary priority effects in habitats created via natural processes may not influence evolutionary priority in anthropogenically converted habitat.

In summary, we have provided evidence that evolutionary priority effects can shape communities in new habitats created by anthropogenic disturbance, although environmental conditions have different influences on evolutionary priority effects in secondary than in primary grasslands. We have also shown that, in primary grasslands, invasion of nonnative species can change the relationship between immigration timing and relative abundance from positive to negative. Thus, in addition to homogenizing the global flora, nonnative species may alter the legacy effect of evolutionary history in community assembly.

Acknowledgements

We thank Branch Creek Station for permission to sample on their land, especially R. Anderson for logistic support and Cardrona Alpine Resort for access. R. Ohlemüller, T. Mannall, X. Li, E. Hüllbusch, K. Collins, J. Glassey, M. Meyer, D. Tuialii, J. Wu and L. Koedyk assisted with data collection and processing. P. B. Heenan, B. Potter, A. S. T. Papadopulos, J. L. Birch and M. D. Pirie assisted with obtaining clade age estimates from the literature. D. R. Leopold assisted with analysis. Comments from three anonymous reviewers greatly improved the paper. Funding for this work was provided by the Royal Society of New Zealand through a Rutherford Discovery Fellowship to B.J.A. and a Marsden Grant to W.G.L.

Author contributions

W.G.L. conceived the idea. B.J.A. and E.H. designed and conducted the field sampling. A.J.B. and A.J.T. compiled and analysed the data. A.J.B., W.G.L. and B.J.A. wrote the manuscript and A.J.T. and T.F. contributed substantially to revisions.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Fig. S1 Diagram of nested sampling design for grassland communities on Mt Cardrona.

Fig. S2 Species and biomass accumulation curves in relation to sampling effort at Mt Cardrona.

Fig. S3 Soil chemistry variables in subset of plots used in stem age analysis in relation to elevation band sampled at Mt Cardrona.

Fig. S4 Relative abundance of the 11 plant clades with a stem age observed both above and below the historic treeline in relation to clade age and its interactions with nonnative biomass and soil resource availability.

Fig. S5 Biomass by provenance, soil moisture and soil fertility in subset of plots used in crown age analysis in relation to elevation band sampled at Mt Cardrona.

Fig. S6 Soil chemistry variables in subset of plots used in crown age analysis in relation to elevation band sampled at Mt Cardrona.

Fig. S7 Relative abundance of the 11 plant clades with a crown age observed both above and below the historic treeline in relation to clade age and its interactions with nonnative biomass and soil resource availability.

Fig. S8 Older plant clades are more diverse on Mt Cardrona and throughout New Zealand.

Fig. S9 Relative abundance of nonnative plant species on Mt Cardrona in relation to naturalisation date in New Zealand.

Table S1 Parameter estimates for models of relative abundance of the 11 plant clades observed both above and below the historic treeline