Climate predicts the proportion of divaricate plant species in New Zealand arborescent assemblages

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ABSTRACT

Aim Puzzling features of plants are sometimes explained as legacies of co-evolution with extinct herbivores. One example is the convergent evolution of a small-leaved, twiggy ‘divaricate’ form in > 50 woody species in New Zealand. This growth form was first interpreted as a response to the Plio-Pleistocene onset of frosty, droughty environments, but opinion now favours the hypothesis that it arose as a defence against large herbivorous birds (moa). It has been argued that the extinction of moa during the last millennium has left divaricate plants at risk of being out-competed by faster growing broadleaved competitors, yet their current abundance in some habitats suggests this growth form might confer other advantages besides protection against avian browsing. We aimed to clarify the adaptive significance of the divaricate growth form by identifying environmental correlates of its geographic distribution in New Zealand.

Location The main islands of the New Zealand archipelago, spanning latitude c. 34.5–47° S.

Methods We used generalized additive models to examine the environmental correlates of the proportion of local tree and shrub assemblages contributed by divaricate species, on 1152 0.04 ha plots distributed across a wide range of climate and landforms.

Results A model with four climatic variables explained 37% of the observed variation. Mean minimum temperature of the coldest month was the single best predictor of the proportion of divaricate species in arborescent assemblages, with annual solar radiation, vapour pressure deficit and annual water deficit also contributing to the final model. Divaricates made their largest contributions to assemblages in the rain shadow of the Southern Alps, on sites with cold winters, low solar radiation and significant vapour pressure deficits, where potential evapotranspiration exceeds precipitation by > 130 mm. No physiographic variables (e.g. slope) contributed to the final model.

Main conclusions The distribution of divaricate plants suggests they cope with frosty, droughty environments better than most other elements of New Zealand’s arborescent flora. This may reflect selection for both (1) physiological resistance to frost and drought and (2) deterrence of herbivores, as climatic constraints on plant growth rates probably leave seedlings exposed for longer to ground-dwelling browsers. However, the widespread persistence of divaricate plants during the c. 450-year hiatus between the extinction of moa and the onset of widespread browsing by introduced ungulates suggests that even in the absence of large herbivores, divaricates are well adapted to frosty, droughty environments.
INTRODUCTION

Quaternary faunal extinctions resulting from the spread of humans around the globe are thought to have altered vegetation structure and function in many regions (Birks, 2005; Johnson, 2009; Doughty et al., 2015a). Moreover, puzzling features of plant species or plant assemblages are often claimed as legacies of co-evolution with large now-extinct vertebrate herbivores. The most celebrated examples are the large fruits and seeds of certain Neotropical trees that appear to lack effective dispersal vectors in contemporary ecosystems (Janzen & Martin, 1982; Guimarães et al., 2008). Broken co-evolutionary links have also been invoked to explain the prominence of light-demanding trees and thorny shrubs in the European flora (Bakker et al., 2004), and ontogenetic trends in spinescence (Janzen & Martin, 1982; Clark & Burns, 2015). These patterns attributed to now-defunct co-evolutionary interactions have been termed ‘ecological anachronisms’ (Barlow, 2002).

A notable case of convergent evolution in the New Zealand flora – the divaricate growth form – has also been attributed to co-evolution with now-extinct herbivores (Greenwood & Atkinson, 1977). The term ‘divaricate’ has been applied to over 50 woody species from 17 different families (Greenwood & Atkinson, 1977), characterized by small leaves, long internodes and wide branching angles, often resulting in an interlacing crown (Fig. 1). Divaricating branches have high tensile strength and are tougher than those of broadleaved congeners (Pollock et al., 2007) or adults in the case of heteroblastic species (Bond et al., 2004). Although there have been diverse opinions on how to define them (see Kelly, 1994), divaricates account for c. 10% of New Zealand’s woody flora, including c. 10 heteroblastic tree species that are divaricate only as juveniles (Greenwood & Atkinson, 1977). Few exact equivalents grow outside of New Zealand, but Bond & Silander (2007) have drawn attention to the abundance of a similar ‘wire plant’ syndrome in the thickets of semi-arid south-western Madagascar. Although divaricate shrubs occur in semi-arid Patagonia and in Tasmania, most have spines (McQueen, 2000; Thompson, 2010; Stajsic et al., 2015), unlike the great majority of New Zealand divaricates.

The divaricate growth form is the single most controversial feature of the New Zealand flora (Lee et al., 2010; McGlone et al., 2010). It was first suggested that it conferred resistance to climatic adversity, and may have arisen in response to the Plio-Pleistocene onset of cold, dry environments (Diels, 1897; Cockayne, 1912). Wardle (1963) also favoured a climatic explanation, emphasizing drought as the main selective force. McGlone & Webb (1981) viewed the divaricate form as the response of a geographically isolated and essentially subtropical flora to the cyclic imposition of glacial and interglacial climates, and discussed mechanisms by which it might enable plants to cope with the unpredictable occurrence of frost, wind and drought in the highly changeable oceanic climates of modern New Zealand. The presence of a divaricate juvenile phase in some heteroblastic tree species could reflect the greater severity of frost close to the ground (Howell et al., 2002), as well as the greater exposure of shallow-rooted juveniles to soil water deficits (Wardle, 1963). Experimental tests of several variants of the climatic hypothesis have mostly proved inconclusive (Kelly & Ogle, 1990; Darrow et al., 2002; Howell et al., 2002; Lusk & Clearwater, 2015).

In contrast, Greenwood & Atkinson (1977) proposed the divaricate form arose in response to unique browsing pressures in New Zealand, where vertebrate herbivore assemblages were dominated entirely by birds, principally nine species of ratites (moa) that were driven to extinction shortly after the arrival of humans in the late 13th century (Anderson, 2003; Perry et al., 2014). Although contemporary New Zealand ecosystems lack exact functional analogues of extinct moa, some (but not all) divaricate plants are avoided by introduced ungulates (Pollock et al., 2007; Lusk, 2014), suggesting the divaricate form has some generalized anti-browsing attributes. In some of the most influential work on the topic to date, Bond et al. (2004) showed that extant ratites (emu and ostrich) were unable to feed effectively on the divaricate juvenile forms of two heteroblastic New Zealand trees, but rapidly consumed adult foliage of the same species. It has been argued that the extinction of moa during the last millennium has left divaricate plants at risk of being out-competed by faster growing broadleaved competitors (Bond et al., 2004).

However, the continued abundance of divaricates in some habitats (e.g. Clarkson & Clarkson, 1994; McGlone et al., 2010), 500–600 years after the extinction of moa, suggest this growth form might confer other advantages besides protection against avian browsing. Moreover, the frequent hybridization of divaricates with non-divaricate congeners (Rattenbury, 1962; Godley, 1985) suggests most divaricates diverged only recently from broadleaved ancestors (Fig. 1), consistent with a Plio-Pleistocene origin (McGlone & Webb, 1981); this evidence of a relatively recent origin is difficult to reconcile with an explanation based solely on browsing by moa, whose ancestors apparently reached the New Zealand landmass at least 60 Ma (Phillips et al., 2010). Although this debate remains unresolved, the moa-browsing hypothesis has resonated

Keywords
drought, frost, generalized additive model, megafaunal legacy, moa-browsing hypothesis, plant–herbivore interactions
internationally, and divaricate plants have been widely reported as a legacy of extinct vertebrate herbivores (Barlow, 2002; Johnson, 2009; Hansen et al., 2010).

Determining the adaptive significance of the divaricate form is vital for understanding the ecological status of these plants in contemporary New Zealand (Bond et al., 2004). If it does confer resistance to frost, drought or other environmental stresses (Diels, 1897; Cockayne, 1912), this should be reflected in the present-day geographic distribution of divaricate plants. Although Greenwood & Atkinson (1977) noted that divaricate plants are found in a wide range of habitats, they recognized that their distribution across New Zealand landscapes is far from uniform (see also Wardle, 1985; McGlone et al., 2010). However, there has yet to be a quantitative analysis of their distribution in relation to present-day environmental factors. Here, we use generalized additive models (GAMs; Hastie & Tibshirani, 1990) to examine the influence of climatic, physiographic and other environmental variables on the proportion of tree and shrub assemblages contributed by divaricate species. We hypothesized that divaricates would contribute most to assemblages on sites subject to low minimum temperatures, and/or appreciable atmospheric or soil water deficits.

Figure 1 Seedling silhouettes (c. 400 mm tall) of two common New Zealand divaricate species and interfertile broadleaved congeners.

Myrsine divaricata  M. salicina

Melicytus micranthus  M. ramiflorus
MATERIALS AND METHODS

Study area and sites

The three main islands of New Zealand span c. 12.5° of latitude, from 34.5° to 47° S. The South Island is mountainous; the main axial ranges running the length of the island including many peaks > 2000 m (see Fig. S1 in Supporting Information). Quaternary glaciation has been influential in shaping South Island landforms, and extensive outwash plains occur to the east of the ranges. On the North Island the ranges are lower, and only three young andesitic cones exceed 2000 m. Hill country makes up much of the North Island, but an extensive rhyolitic plateau occupies the centre, and several of the major rivers have formed sizeable alluvial plains and terrace systems. The smaller Stewart Island is mostly undulating, with low ranges not exceeding 1000 m elevation.

Although New Zealand climates are broadly described as oceanic temperate, they encompass a wide range of temperature regimes and annual precipitation (Garnier, 1958; NIWA, 2001). Mean annual temperatures range from < 5 °C at high elevations in the south to c. 16 °C in the far north. Frosts are rare on western coasts of the North Island, but occur throughout most of the year in intermontane basins in the eastern South Island and in the central North Island. Rainfall patterns on the South Island are dominated by the strong orographic effect of the axial ranges (Southern Alps): the moisture-laden prevailing westerly winds bring > 2000 mm annually to most sites west of the main divide (and often > 4000 at high elevations), whereas the eastern lowlands in the lee of the Southern Alps mostly receive < 1000 mm. The west-to-east precipitation gradient is less marked in the North Island, because of the lower and more complex relief (see Fig. S1). Some alluvial lowland areas in the east and south-west of the North Island receive < 1000 mm; at the other extreme, > 2000 mm falls on the major volcanoes and on most ranges above 1000 m elevation. Many North Island sites are subject to a weak summer rainfall minimum, but precipitation is evenly distributed throughout the year over most of the South Island. Stewart Island is wet (> 1500 mm) and cool throughout, with a strong maritime influence buffering daily and seasonal temperature variation.

Before human arrival in the late 13th century, most of New Zealand was covered by closed forest, with tussock grasslands above tree line, and extensive wetlands in some lowland areas (Wardle, 1991). Lowland plains and terraces of the North and South Islands have been almost entirely converted to intensive agriculture, with only small scattered forest remnants surviving. The only exception to this generalization is the wet western coast of the South Island, where extensive lowland forests remain on poorly drained terraces. Lowland hill country has been largely deforested in the east of both main islands, but extensive native forest cover still remains on this landform in the western North Island and the southern South Island. The main axial ranges are still largely covered in primary forest, although human set fires have caused an expansion of tussock grasslands. Extensive seral shrublands occur on both main islands. In contrast to the North and South Islands, Stewart Island remains largely forested.

Sites and species

Species lists were obtained from 0.04 ha plots sampled for the New Zealand Carbon Monitoring System (Payton et al., 2004). These comprised 1152 forest and shrubland plots, distributed throughout the three main islands of New Zealand. All tree and shrub species were scored as either divaricate or non-divaricate, mostly according to table 1 in Greenwood & Atkinson (1977). We included monocotyledonous trees and tree ferns in our list of tree and shrub species. We then computed the proportion of total tree and shrub species richness contributed by divaricate species on each plot. Nomenclature follows the New Zealand Plant Names Database, available at http://nzflora.landcareresearch.co.nz/.

Environmental predictors

Candidate environmental predictors (Table 1) were estimated from environmental surfaces held in geographic information systems (GIS). Most of these variables were taken from Leathwick et al. (2003) and Overton et al. (2009), and include climatic, geographic and vegetation parameters sometimes found to have value in predicting species distributions and/or patterns of species richness. These variables included derived predictors that might be more directly related to plant physiology and ecology, such as vapour pressure deficit and seasonality of temperatures; these derived predictors act as physiologically informed interactions between the fundamental climate layers. Distance from the coastline serves as a proxy for a suite of related environmental variables including continentality (thermal amplitude) and exposure to wind, and outperforms direct estimates of those variables (Overton et al., 2009).

Modelling

Leathwick et al. (1998) showed that tree species richness in New Zealand is highest on warm, moist, sunny sites. In contrast, McGlone & Webb (1981) hypothesized that ‘the majority of divericating plants and heteroblastic juveniles in the New Zealand flora have evolved in response to lowland and montane environments which are unsuitable for normal tree growth because of the high and unpredictable incidence of frost, wind and drought’. According to this hypothesis, we would expect divericcate species to show significantly different patterns of richness from tree species in general, and to dominate assemblages on sites exposed to high levels of frost, drought and/or wind. Accordingly, we used GAMs, in S-PLUS (Insightful, Seattle) and a logit link function to model the influence of environmental variables on the proportion
variables were removed because of high (r) correlations with other variables. We started with a model containing all remaining candidate variables and used backwards and forwards stepwise selection with Akaike’s information criteria (AIC) to select a model. We then evaluated model performance using k-fold cross-validation with six folds. This consisted of randomly assigning each observation to a one of six folds. Each fold is in turn withheld from the data and the model fitted on the other five folds, and the predicted and observed values compared for the withheld data. This is repeated for all folds, until all observations have been compared to predictions made from models in which the observation was not included in the fitting process.

RESULTS

General description of data

A total of 38 divaricate tree and shrub species were found on the 1152 study plots (see Table S1). The most frequent of these were *Coprosma rhamnoides* (38% of plots), followed by *Myrsine divaricata* (36%).

Model selection and performance

A preliminary model with 13 variables (eight climatic variables, four physiographic variables and total aboveground carbon) explained 45% of deviance. A reduced model (Figs 2–4) that maximized cross-validation performance was considerably more parsimonious, with four climatic variables and a somewhat lower explained deviance of 37%; the correlation between observed and predicted was 0.64 under validation and 0.63 under sixfold cross-validation (Fig. 3). This reduced model is used for all further results and discussion and is referred to below as the ‘final’ model.

Relative importance of environmental predictors

The relative importance of the predictor variables in determining divaricate representation in arborescent assemblages is indicated by the ‘alone’ and ‘drop’ contributions (sensu Lehmann et al., 2002) of the four variables included in the final model (Fig. 2). The ‘alone’ contributions show the explanatory power of each variable separately, whereas the ‘drop’ contributions show the loss of explanatory power when each variable in turn is dropped from the final model. When two variables overlap in their explanatory power, one or both may have a high ‘alone’ contribution, but relatively low ‘drop’ contribution.

July minimum temperatures were the best single predictor of divaricate representation (accounting for 26.3% of deviance), although solar radiation and annual water deficit also had considerable explanatory power (Fig. 2b). Dropping each predictor variable in turn (Fig. 2a) confirmed winter minimum temperatures as the variable with most explanatory power, its removal from the model resulting in a 20.7% loss of the model’s explanatory power. In contrast, dropping annual water deficit caused only a 3.5% loss of power, showing the effect of this variable could be largely accounted for by a combination of the other predictors in the final model.

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<th>Table 1 Environmental predictors explored as candidates for generalized additive models to explain distribution of divaricate species in New Zealand. Asterisks show the four predictors included in the final model.</th>
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Environmental correlates of divaricate representation

Divaricates made their largest proportional contributions to arborescent assemblages on sites with low July minimum temperatures, though this relationship was not monotonic (Fig. 4). The proportion of divaricate species in assemblages decreased linearly with increasing solar radiation, and was positively correlated with annual water deficit and October vapour pressure deficit.

Geographic patterns in richness of divaricate species throughout New Zealand (Fig. 5b) differed from those shown by total richness of arborescent species (Fig. 5a). Total richness of arborescent species was highest in the northern half of the North Island and the western South Island, and lowest in the south-eastern South Island. Divaricate richness was highest in the South Island, with an average of 3.6 species per plot; all plots with eight or more divaricate species were in the South Island. Although divaricate species richness was much lower on average (1.8) in the North Island, five to seven species were present on some plots in the central and eastern North Island. Only one plot in the northern North Island (north of lat. 37.5° S) harboured more than three divaricate species. Divaricate species richness averaged 3.3 per plot on Stewart Island.

The net result of these patterns is that divaricates made their largest proportional contributions to arborescent assemblages richness in eastern and inland parts of the South Island, and least (generally < 20% of arborescent species) in the northern and western North Island (Fig. 5c). Although divaricate representation was moderately high (25–45%) on some plots in the central and eastern North Island, all plots where > 50% of arborescent species were divaricate were in the South Island, most of them on eastern or inland sites with ≤ 10 species arborescent species in total. Divaricates contributed ≤ 35% of arborescent species on all plots on Stewart Island.

DISCUSSION

Divaricate species dominate arborescent assemblages on frosty and droughty sites (Figs 2 & 4), especially in the eastern and inland South Island in the lee of the Southern Alps (Fig. 5). Divaricates are also well represented in the central North Island, where the frost-free period is < 4 months on many sites (NIWA, 2015), and in the lowlands of the eastern North Island, where potential evapotranspiration often exceeds annual rainfall; earlier work, sampling much larger areas than our 0.04 ha plots, reported > 20 divaricate species at some sites in the central and eastern North Island (Clarkson & Clarkson, 1994). The distribution of divaricate species richness thus differs appreciably from that of total richness.
of arborescent species, which is highest on rainy sites on low
mountain ranges in the northern North Island, and on the
west coast of the South Island (Fig. 5). The distribution of
divaricates differs more markedly still from richness of
broadleaved canopy trees, which previous work has shown to
peak on warm, moist sites in the northern North Island
(Leathwick et al., 1998).

It is unclear why divaricate representation also showed a
negative partial correlation with annual solar radiation
(Fig. 4). Again, this pattern contrasts with that previously
shown for broadleaved canopy tree richness in New Zealand,
which is positively correlated with solar radiation (Leathwick
et al., 1998). There is a general southward decline in annual
solar radiation throughout New Zealand (NIWA, 2001), and
the negative relationship of divaricate representation with
solar radiation might simply reflect the small size of the
regional pool of broadleaved canopy species south of about
latitude 42° S, a floristic pattern possibly resulting from the
region’s Plio-Pleistocene history of repeated severe glaciation
(McGlone et al., 2010).

The moderate explanatory power of our final model (37% of
deviance) probably reflects the small plot size in our data
set (400 m²). Small plots capture a variable subset of the
species found on larger plots, resulting in more variable
estimates of metrics such as the proportion of divaricate
species in an assemblage. Similar modelling studies of plant
species richness data from larger plots have reported higher
explained deviance values of 50–70% (Bhattarai & Vetaas,
2003; Moser et al., 2005).

The climatic signal in the representation of divaricates
indicates this growth form in some way helps plants deal
with the aseasonal occurrence of frost and drought (Diels,
1897; Wardle, 1963; McGlone & Webb, 1981). Divaricate
plants grow more slowly than their broadleaved congeners
(Gamage, 2011) as a result of their smaller leaf area ratios
(Christian et al., 2006), and landscape partitioning between
the two might reflect trade-offs between competitiveness in
benign climates versus resistance to climatic stresses. In con-
trast to the pronounced and stable seasonality of continental
climates, New Zealand’s oceanic climates are characterized by
a narrow annual temperature range but wide day-to-day
variation (Garnier, 1958; Sturman & Tapper, 2006); on many
lowland sites in the central North Island and eastern South
Island, opportunities for carbon gain and growth are inter-
spersed with frosts throughout much of the year. Similarly,
drought is not a consistent feature of any particular season
in New Zealand, and while rainless periods can affect low-
land sites anywhere in the country, they occur frequently in

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**Figure 4** The partial response of divaricate representation in arborescent assemblages in New Zealand to each predictor variable is shown on the Poisson link scale. Sample density is shown by hash marks on the x-axis of all graphs. Standard errors are shown as dash-dot lines. Model formula = divaricate representation ~ s(Deficit, 1) + s(VPD, 1) + s(Radiation, 1) + s(Tmin, 3), family = binomial. Predictor variables are explained in Table 1.
Figure 5 Distribution of (a) total arborescent species richness across 1152 plots on the main islands of New Zealand, (b) divaricate species richness and (c) the proportion of arborescent species contributed by divaricate plants on each plot.
eastern districts in the lee of the main axial ranges during El Niño years, which are characterized by unrelenting westerly winds (Mullan, 1996). The weak seasonality of New Zealand climates helps explain why deciduousness is much rarer than on the northern continents (McGlone et al., 2004), and McGlone & Webb (1981) argued that the divaricate form enables plants to cope with this changeability – in particular, the unpredictable occurrence of frost. Although weakly seasonal climates are also found in other maritime temperate regions such as Tasmania and Britain, the floras of those realms have been strongly influenced by their intimate connections to large continents harbouring more seasonal and/or semi-arid environments, in contrast to New Zealand’s prolonged isolation (McGlone et al., 2016).

It remains unclear how the divaricate form confers resistance to intermittent frost or drought. Howell et al. (2002) showed that the twiggy outer canopy of some divaricates protected the inner foliage against photo-inhibition on frosty mornings, but no broadleaved species were included for comparison (Lusk, 2002). Leaf energy balance theory predicts small leaves, such as those of divaricates, should be more closely coupled to air temperatures than large leaves and thus less vulnerable to overheating in dry, sunny conditions (Parkhurst & Loucks, 1972). This effect was confirmed by a recent study of South African Proteaceae, showing that 10-fold variation in leaf width was associated with a $c. 5^\circ C$ range in temperatures of leaves exposed to strong radiative heating at low wind speeds (Yates et al., 2010). The same theory predicts that small leaves should also be less vulnerable to chilling on cold, clear nights (Leuning, 1988), although comprehensive tests of this prediction are lacking. Although deciduousness is adaptive in environments with strongly seasonal patterns of freezing or drought (Kikuzawa, 1991; Givnish, 2002), the small leaves of divaricates might represent a more effective way of coping with the irregular occurrence of these stresses in New Zealand’s less predictable climate. However, many small-leaved plants in New Zealand and elsewhere are non-divaricate, and the effect of leaf size on leaf energy balance does not explain the wide-angled branching of divaricates, or the toughness of their fine branches (Bond et al., 2004).

In addition to the direct physiological challenges posed by frost and drought, climatic constraints on plant growth may also leave juvenile plants more exposed browsing by ground-dwelling herbivores. On productive sites with a long growing season, fast growth might be an effective means of coping with ground-dwelling herbivores: for example, most pioneer trees in tropical rain forests lack well-developed physical or chemical defences, and depend mainly on fast growth to cope with herbivores (Coley, 1983). Similarly, Anton et al. (2015) reported that seedlings of the small broadleaved tree Aristotelia serrata planted on a largely frost-free coastal North Island site often grew 100–150 cm in height per year, implying that, given ample light and moisture, they could escape from the browse zone of ground-dwelling herbivores within as little as 2 years. In contrast, in the south-eastern South Island, where the frost-free period is much shorter, another study found that annual height growth of A. serrata seedlings was usually < 40 cm (Russell, 1968). The frosty, droughty climates resulting from the combination of global cooling and uplift of the Southern Alps may thus have selected not only for physiological resistance to cold and drought, but also for physical defences against browsing – especially in lineages with nutrient-rich, short-lived leaves, such as most genera that have spawned divaricate species (e.g. Lee & Johnson, 1984; Lee, 1988; Duncan et al., 2003). Globally, physical defences against vertebrate browsing are common in environments where plant growth is restricted by water availability, including thorny African savannas and Patagonian shrublands, and southern Madagascar where a ‘wire plant’ syndrome similar to the New Zealand divaricate form has been documented (McQueen, 2000; Bond & Silander, 2007).

An important unresolved question in New Zealand ecology is the extent to which introduced ungulates now occupy the browsing niches previously filled by moa (Forsyth et al., 2010; Lee et al., 2010). A cafeteria experiment reported that both deer and avian herbivores (ostriches) generally avoided divaricate and other small-leaved species (Pollock et al., 2007). Although divaricates are by no means exempt from mammalian browsing in the wild (Clarkson & Clarkson, 1994; Clarkson et al., 2003), a list of 18 native arborescent species identified by Forsyth et al. (2002) as preferred by introduced ungulates includes 12 fast-growing broadleaved small trees and shrubs, and no divaricates. Nevertheless, the current distributions of many divaricate species suggest widespread survival during the c. 450-year ‘herbivory hiatus’ (Lee et al., 2010) between the extinction of moa and the spread of introduced ungulates, when divaricate plants may have been exposed to more competition from fast-growing broadleaved species. Two overstorey trees with divaricate juvenile forms (Prumnopitys taxifolia, Elaeocarpus hookerianus) live long enough for their adults to have survived this hiatus even in the event of new recruitment being curtailed by moa extinction, but these species are atypical. The few demographic data available on smaller divaricate trees and shrubs show ages not exceeding 100 years (Clarkson & Clarkson, 1994; Molloy & Clarkson, 1996; Molloy et al., 1999) implying that several generations would have occurred during the herbivory hiatus. This indirect evidence, as well as early botanical accounts of the widespread abundance of divaricates before introduced ungulates became an important driver of vegetation change (Buchanan, 1868; Cockayne, 1912), suggest that, even in the absence of large herbivores, divaricates continued to be well adapted to frosty, droughty environments in New Zealand (cf. Bond et al., 2004; Lee et al., 2010).

Our results are consistent with climate having played a major role in the evolution of the divaricate form (Diels, 1897; Cockayne, 1912; McGlone & Webb, 1981). Although the debate has tended to be polarized, some authors have suggested that a synergy of climatic and browsing pressures might ultimately be implicated (Wardle, 1985; Cooper et al., 1993). This might have taken the form of dual selection pressures arising from the Pliocene onset of frosty, droughty
climates: (1) direct physiological challenges posed by intermittent frost and drought and (2) greater exposure of juveniles to ground-dwelling herbivores as a result of climatic constraints on plant growth rates. Although the extinction of moa may have altered the distributions of some divaricate plants (Greenwood & Atkinson, 1977; Bond et al., 2004; Lee et al., 2010), the continuing dominance of this growth form in some contemporary assemblages shows it is well adapted to frosty and droughty environments in present-day New Zealand (Figs 4 & 5). Moreover, in contrast to the restricted distributions of some Neotropical plants thought to have lost megaфаunal co-evolutionary partners (Johnson, 2009; Doughty et al., 2015b; Muñoz-Concha et al., 2015), some divaricate species are among the most widespread native woody plants in New Zealand, three of them occurring on over a third of all plots (see Table S1).

Determining the extent to which introduced ungulates now emulate the former impact of moa on New Zealand vegetation is critical for plant conservation strategies (Atkinson, 2001; Hughey & Hickling, 2006). Climate change is an added complication: frost frequencies are predicted to decrease markedly throughout much of New Zealand during the 21st century, whereas the frequency of drought is predicted to increase in northern and eastern lowland areas (Mullan et al., 2001). Clarifying the net effect of these trends on potential habitat availability for divaricate plants is another important challenge.

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REFERENCES


**SUPPORTING INFORMATION**

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

**Appendix S1** List of divaricate species found on study plots, and relief map of the main islands of New Zealand.

**BIOSKETCHES**

Chris Lusk (CHL) is a plant ecologist who has worked in Chile, Australia and New Zealand. He is currently interested in reconciling some of the quirks of New Zealand’s flora and vegetation with ecological theory.

Matt McGlone (MSM) is a plant ecologist and biogeographer who uses palaeoecological perspectives to inform interpretations of contemporary New Zealand and Southern Hemisphere vegetation.

Jake Overton (JMO) is an ecological modeller who is part of the Biodiversity and Conservation team at Landcare Research.

Author contributions: C.H.L., J.M.O. and M.S.M. developed the idea; J.M.O. accessed vegetation and environmental data and carried out statistical modelling; C.H.L. wrote most of the paper, supported by M.S.M. and J.M.O.

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