Divaricate plants resist ungulate browsing in a forest remnant on the North Island of New Zealand

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Abstract

It has been suggested that divaricate plants are an anachronism in contemporary New Zealand, because of the extinction of browsing birds (moa) that may have influenced their evolution, and because the divaricate form is not an effective defence against introduced browsing mammals. This article infers the relative susceptibilities of divaricate, broadleaved and conifer species to ungulate browsing, by measuring tree diameter distributions in a forest remnant fenced in the late 1970s after a century of unimpeded access by livestock. The 26 ha remnant, at Pehiri in the eastern North Island, spans a range of landforms from river flats (favoured by podocarps and divaricates) to hillslopes where broadleaved species predominate. The commonest broadleaved species (*Alectryon excelsus*, *Melicytus ramiflorus*, *Hedycarya arborea*) had empty or under-represented diameter classes in the 5 to 20 cm range, consistent with reduced regeneration during the century of unrestricted browsing. In contrast, the diameter distributions of the common divaricates *Elaeocarpus hookerianus*, *Myrsine divaricata* and *Melicope simplex* were well-described by power functions, suggesting more-or-less continuous regeneration; this was also true of the commonest conifer, *Dacrycarpus dacrydioides*. Our results suggest the divaricate growth form is well-adapted to contemporary New Zealand environments: as well as possibly enabling plants to cope with certain physical environments, it deters browsing by least some of the mammalian herbivores introduced since European settlement. As browsing mammals were clearly not involved in the origin of the divaricate growth form in prehistoric New Zealand, its current function in resisting ungulate browsing may be viewed as an example of exaptation.

Key words: browsing preferences - divaricate plants - evolutionary anachronisms - extinct megafauna - mammalian browsing - moa browsing hypothesis - podocarp regeneration - regeneration failure.

Introduction

Few features of the New Zealand flora and vegetation have fired scientists' imaginations like divaricate plants. For over 100 years, ecologists and botanists have debated the adaptive significance of the divaricate growth form that occurs in many shrubs and juvenile trees from diverse families (e.g. Wardle 1985; Lee et al. 2010; McGlone et al. 2010). According to Kelly (1994), divaricates can be defined as possessing a distinctive combination of (1) interlaced, wide-angled branches, (2) small, widely-spaced leaves (<60 mm^2), and (3) somewhat larger leaves towards the interior of the plant. Although exact equivalents outside New Zealand appear to be uncommon, Bond and Silander (2007) have reported a similar "wire plant" syndrome in 36 genera of woody plants from southern Madagascar.

Explanations of the abundance of the divaricate growth form in New Zealand have invoked two types of selective forces. Diels (1897) and Cockayne (1912) suggested this growth form developed in response to harsh Pleistocene climates; subsequent authors have explored its possible role in protecting plants against frost, drought and photoinhibition (e.g. McGlone & Webb 1981; Wardle 1985; Howell et al. 2002), although there is no conclusive evidence about the physiological mechanisms involved (Lusk 2002). In contrast, Greenwood and Atkinson (1977) argued that the divaricate growth form evolved in response to the browsing pressures exerted by New Zealand's unusual prehistoric herbivore assemblages, dominated by flightless birds (moa). Although often presented as competing hypotheses, these two explanations should not be viewed as mutually exclusive, the form and function of organisms inevitably being shaped by multiple selection pressures (Gould & Vrba 1982; Lowell 1987; Jones et al. 2005).

Strong support for the moa browsing hypothesis emerged from an experiment comparing browsing behaviour of extant relatives of moa (ratites) with that of a goat (*Capra hircus*) (Bond et al. 2004). Ostriches (*Struthio camellus*) and emus (*Dromaius novaehollandiae*) had difficulty feeding effectively on the divaricate juvenile foliage of two New Zealand tree species that was quickly consumed by the goat. The authors concluded that the divaricate habit is an "anachronism" (cf. Janzen & Martin 1982) in contemporary New Zealand, and is ineffective in deterring browsing by ungulates. Burdened with a growth form that strongly constrains height growth, but that may no longer be an effective defence, divaricate plants might therefore be expected to be in decline (Bond et al. 2004).

Despite this expectation, the current abundance of divaricate plants in some habitats, at least 450 years after extinction of moa, suggests they cope well with contemporary selection pressures (Clarkson & Clarkson 1994; McGlone et al. 2010). New insight into this situation has been provided by a more recent cafeteria experiment comparing dietary preferences of ungulates and extant ratites, the latter used as a proxy for extinct moa (Pollock et al. 2007). That study found that divaricate species were actually more consistently avoided by red deer (*Cervus elephus scoticus*) than by ostriches, suggesting that, regardless of its

evolutionary origins, the divaricate growth form may now afford some protection against browsing in contemporary New Zealand ecosystems (see also Wardle 1985), where most vertebrate folivores are mammals rather than birds.

This article provides further evidence of the adaptive value of the divaricate growth form in contemporary New Zealand ecosystems. I compare the population structures of eight of the commonest tree species (divaricate and broadleaved angiosperms, as well as conifers) in a North Island forest remnant about 35 km west of Gisborne, and show that a ~100-year history of browsing by livestock appears to have had less impact on the recruitment of divaricates than on that of their broadleaved associates.

Methods

Study site

Sampling was carried out in a 26 ha forest remnant located on the south bank of the Waikura River (38°38'25"S, 177°40'54"E), on Te Aroha Station near Pehiri. This remnant occupies a small part of the floodplain and a series of terraces and hillslopes, in total spanning a range of elevation of about 100 m. The forest on the floodplain and the lower terrace is dominated by podocarps (mainly *Podocarpus totara* and *Dacrycarpus dacrydioides*) and divaricates. On the upper terraces and hillslopes, both overstorey and understorey dominance shifts to broadleaved species, especially *Alectryon excelsus* and *Melicytus ramiflorus*

Table 1. Principal overstorey and understorey woody species on different landforms at Pehiri. Asterisks denote species that are divaricate either as juveniles or at all stages. Nomenclature follows Allan Herbarium (2002-2013).

	Floodplain	Lower terrace	Upper terraces, hillslopes
Podocarpus totara	X	X	X
*Prumnopitys taxifolia**	X	X	X
Dacrycarpus dacrydioides	X	X	X
Beilschmiedia tawa			X
Hedycarya arborea			X
Macropiper excelsum			X
Melicytus ramiflorus		X	X
*M. micranthus**	X	X	
Knightia excelsa			X
*Elaeocarpus hookerianus**	X	X	
*Plagianthus regius**	X		
Hoheria sexstylosa	X	X	X
*H. angustifolia**	X		
*Melicope simplex**	X	X	X
Alectryon excelsus			X
Nestegis lanceolata	X	X	
*Myrsine divaricata**	X	X	

(Table 1). Nomenclature follow Allan Herbarium (2002-2013).

The forest remnant is currently fenced to exclude livestock, but has a complex recent history of disturbance by browsing and fire. The land that was to become Te Aroha Station was first surveyed in 1876 (Hickson 1876), and livestock farming in the area began from 1878 when sales to settlers began (Hall 2009). Livestock therefore had about 100 years of access to the site before the present forest remnant was fenced in the late 1970s (Phillip Steele[1] , pers. comm). Although sheep (*Ovis aries*) are currently farmed at Te Aroha, cattle (*Bos taurus*) were originally the main source of income, as mobs of wild dogs made sheep farming impossible. Red deer and brushtail possums (*Trichosurus vulpecula*) are both common in the area and known to browse native vegetation in the remnant. A prevalence of stems < 50 cm diameter in the overstorey (Fig. 1), and the presence of fire scars on the larger trees scattered throughout the remnant (especially on the lower terrace) suggest that much of the forest has regenerated following partial destruction by fire during historic times; however, fire events have not been dated.

Sampling

Tree diameter distributions were quantified on six 400 m² plots. In the lower parts of the reserve dominated by podocarps and divaricates, one plot was located on the floodplain and two on the more extensive area of forest on the lower terrace. In the upper parts of the reserve dominated by broadleaved species, two plots were located on terraces, and one

on a hillslope. Plot sites were chosen at random points on transects run parallel to the long axis of landforms. The default dimensions were 20m x 20m, but 40m x 10m plots fitted better into the narrow strip of forest remaining on the floodplain, and onto the upper terraces. All woody plants taller than breast height were sampled, with one exception: due to the overwhelming abundance of *Melicytus ramiflorus* < 5.0 cm diameter on one plot on the lower terrace, this size class of this species was subsampled on 25% of that particular plot. Although *M. ramiflorus* in particular was often multi-stemmed, only the largest stem of each individual was counted.

Population structure analysis

The continuity of recent regeneration of the commonest divaricate[2], broadleaved and podocarp species was assessed by examining the fit of their diameter distributions to a power function model (Hett & Loucks 1976; Veblen et al. 1979). Populations with a recent history of more-or-less continuous regeneration have diameter distributions that approximate a "reverse-J" structure, with progressively fewer stems in successive diameter classes, being well described by a power function. As well as being used to compare regeneration modes of species (e.g. Veblen et al. 1979), the degree of fit to a power function model can be used to gauge the influence of browsing history on regeneration of different species (e.g. Veblen & Stewart 1980). Accordingly, the linear transformation of the power function model

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[1] Proprietor of Te Aroha Station, Pehiri.

[2] The commonest divaricate species at the site (*Melicytus micranthus*) was omitted from the analysis as it did not exceed 15 cm diameter i.e. was present in only three diameter classes.

$$\ln (y+1) = \ln (yo+1) - b \ln x$$

was applied to those species with at least one individual in each of the first four 5 cm diameter classes, where x is the mid-point of each diameter class, yo is the initial input into the population at time zero, y is the number of stems in each diameter class, and b is the mortality rate. Note that 1.0 was added to the raw abundance data (y values), to make logarithmic transformation of "zero" values possible. This enabled analysis of populations with gaps in their size distributions, i.e. empty diameter classes.

Results

The population structures of the three common divaricate species approximated a reverse-J structure, in general showing progressively fewer stems in successive diameter classes (Fig. 1). The power function model described the population structures of the divaricates well (Table 1: $R^2 > 0.8$ in all cases), suggesting that recent regeneration of all three has been more-or-less continuous. The lack of *Melicope simplex* and *Myrsine divaricata* > 20cm diameter reflects the small maximum size attained by these understorey species (Allan Herbarium 2002-2013).

In contrast, the populations of the three commonest broadleaved angiosperms departed to varying degrees from a reverse-J structure (Fig. 1). *Hedycarya arborea* was represented by abundant saplings < 5 cm diameter, but completely
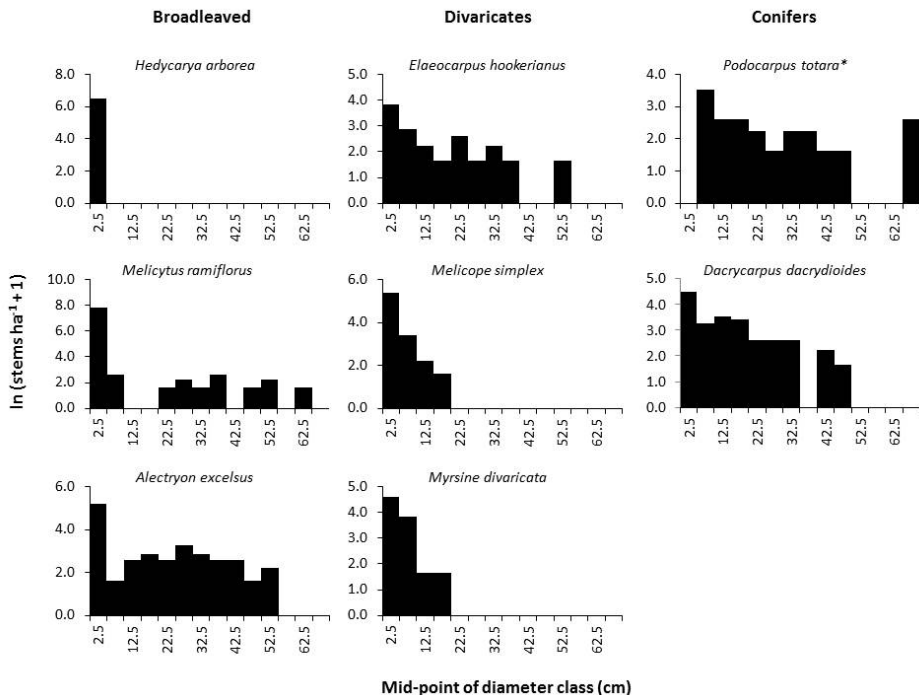

Figure 1. Diameter distributions of common broadleaved, divaricate and conifer species in a forest remnant near Pehiri, New Zealand, obtained from six 400m2 plots. The labels on the x-axis show the mid-points of every second 5cm diameter class.
*One P. totara of 169.0 cm diameter was omitted to avoid including many empty diameter classes.

Table 2. Regression equations fitting the diameter distributions of common divaricate, broadleaved and conifer species at Pehiri to the power function model; n is the number of pairs of x (diameter classes) and y (numbers of stems in diameter classes) variables.

Species	n	Equation	R^2	P <
Conifers				
Podocarpus totara	14	$\ln(y+1) = 2.248 - 0.338 \ln(x)$	0.221	.448
Dacrycarpus dacrydioides	10	$\ln(y+1) = 4.622 - 1.314 \ln(x)$	0.792	.006
Divaricate angiosperms				
Elaeocarpus hookerianus	11	$\ln(y+1) = 3.811 - 1.232 \ln(x)$	0.808	.003
Melicope simplex	4	$\ln(y+1) = 5.328 - 2.726 \ln(x)$	0.999	.002
Myrsine divaricata	4	$\ln(y+1) = 4.831 - 2.385 \ln(x)$	0.938	.061
Broadleaved angiosperms				
Melicytus ramiflorus	13	$\ln(y+1) = 4.662 - 1.619 \ln(x)$	0.599	.030
Alectryon excelsus	11	$\ln(y+1) = 3.905 - 0.733 \ln(x)$	0.574	.065

absent in all larger classes. In contrast, *Melicytus ramiflorus* and *Alectryon excelsus* were represented by a wide range of sizes, including abundant saplings. However, empty or under-represented diameter classes in the 5 to 20 cm range resulted in relatively poor fits of both these species' population structures to the power function model ($R^2 < 0.6$ in both cases). There was a notable difference between the population structures of the two commonest conifers. Despite a lack of stems in the 35-40 cm diameter class, the population of *Dacrycarpus dacrydioides* approximated a reverse-J structure overall (Fig. 1) and so was described quite well by the power function model (Table 2). On the other hand, although *Podocarpus totara* was also generally represented by progressively fewer stems in successive diameter classes, no saplings (< 5 cm diameter) were found on any of the six plots (Fig. 1). As a result, the power function model described the population structure of *P. totara* very poorly (Table 2).

Discussion

The population structures of the three commonest broadleaved species suggest that few individuals of these species established during the century of un-restricted browsing by sheep, followed by a resurgence after fencing in the late 1970s (Fig. 1). The imperfect correspond-ence between the apparent "regeneration gaps" in the diameter distributions of *Melicytus ramiflorus* and *Alectryon excelsus* probably reflects a difference in growth rate. Although no data are available on the juvenile growth of *A. excelsus*, it is almost certainly slower-growing than *M. ramiflorus*, a subcanopy tree known to be one of the faster-growing species in the New Zealand woody flora (Lusk et al. 2013). The lack of *Hedycarya arborea* in all but the smallest size class is puzzling as, like *M. ramiflorus* and *A. excelsus*, this species sometimes attains diameters > 50 cm, and is almost certainly capable of living more than 100 years. Although no *H. arborea* stems > 5 cm diameter were recorded on any of the six plots, the pre-sent abundance of understorey saplings on the upper terraces and hillslopes must reflect dispersal from a small number of parent trees present either somewhere in the same remnant, or in other nearby

forest fragments.

The current floristic composition of the forest at Pehiri also bears the imprint of the recent history of browsing. A number of broadleaved small trees and shrubs typical of lowland North Island forests were not seen anywhere in the remnant, including *Schefflera digitata*, *Pseudopanax arboreus*, *Coprosma grandifolia*, *C. lucida* and *C. robusta*, all of which are known to be preferred by introduced ungulates (Forsyth et al. 2002) and prone to rapid depletion in areas with large ungulate populations (e.g. Mark & Baylis 1982). As these are all short-lived species, almost certainly living less than 100 years, it seems reasonable to surmise they were driven extinct locally during the century of browsing by livestock that appears to have also prejudiced establishment of *M. ramiflorus* and *A. excelsus*.

In contrast, the population structures and high local species richness of divaricates suggest that the period of unrestricted browsing had less effect on these plants. The diameter distributions of the common divaricate species show no evidence of marked fluctuation in recent rates of regeneration (Fig. 1; Table 2). Furthermore, whereas browsing by livestock has likely caused local extinction of several broadleaved small trees and shrubs, at least 21 divaricate species are present at Pehiri (Clarkson & Clarkson 1994), one of the highest figures recorded anywhere in New Zealand. This evidence that the divaricate plants survive ungulate browsing better than their broadleaved competitors is difficult to reconcile with the view that the divaricate growth form is disadvantageous in contemporary New Zealand (cf. Bond et al. 2004); the current presence of ungulates in New Zealand forests may favour at least some divaricate species by reducing competition from faster-growing broadleaved species.

The population structures of the two common conifers suggest that, like divaricates, they are able to regenerate in the presence of browsing by livestock. The diameter distributions of neither *Dacrycarpus dacrydioides* nor *Podocarpus totara* showed evidence of a depression of regeneration during the century of browsing (Fig. 1), consistent with evidence that most New Zealand conifers are avoided by ungulates (Forsyth et al. 2002). In fact, the lack of saplings (< 5 cm diameter) of the latter species may indicate that it was disadvantaged by the exclusion of sheep in the late 1970s, its seedlings perhaps being smothered by the proliferation of fast-growing broadleaved species such as *M. ramiflorus* after fencing. *P. totara* is likely to be a poor competitor as a seedling, as comparative data show it grows more slowly in height than *D. dacrydioides* (and most broadleaved species) in addition to being one of the more light-demanding of New Zealand's conifers (C. H. Lusk & P.J. Bellingham, unpublished).

The results of this study indicate that divaricate plants are well-adapted to at least some present-day New Zealand environments. Strong geographic patterns in the distribution of the divaricate growth form suggest that it enables plants to cope with certain physical environments. For example, both divaricate species richness and the percentage of divaricates in local woody floras increase with increasing latitude (McGlone et al. 2010), however, the basis of these patterns remains poorly understood. On the other hand, the data presented here build on the findings of Pollock et al. (2007) by providing field

evidence that the divaricate growth form protects plants against browsing by at least some introduced ungulates. This may be viewed as an example of exaptation (Gould & Vrba 1982), the co-opting of an existing structure in new functions by natural selection; as browsing mammals do not appear to have been present in the New Zealand archipelago at any stage before human arrival during the last millennium, they cannot have been responsible for the origin of the divaricate growth form. The relative roles of moa browsing and climatic factors in shaping the evolution of this growth form in prehistoric New Zealand remain to be clarified.

Acknowledgements

References

Allan Herbarium. 2002-2013. Ngā Tipu o Aotearoa – New Zealand Plants database. Landcare Research, Lincoln.

Bond, W.J.; Lee, W.G. & Craine, J.M. 2004. Plant structural defences against browsing birds: a legacy of New Zealand's extinct moas. Oikos 104: 500-508.

Bond, W.J. & Silander, J.A. 2007. Springs and wire plants: anachronistic defences against Madagascar's extinct elephant birds. Proceedings of the Royal Society B: Biological Sciences 274: 1985-1992.

Clarkson, B.D. & Clarkson, B.R. 1994. Ecology of an elusive endemic shrub, *Pittosporum obcordatum* Raoul. New Zealand Journal of Botany 32: 155-168.

Cockayne, L. 1912. Observations concerning evolution, derived from ecological studies in New Zealand. Transactions of the New Zealand Institute, pp 1-50.

Diels, L. 1897. Vegetations-Biologie von Neu-Seeland. Botanische Jahrbiicher fur Systematik, Pflanzengeschichte uni Pflanzengeographie 22: 202-300.

Forsyth, D.M.; Coomes, D.A.; Nugent, G. & Hall, G.M.J. 2002. Diet and diet preferences of introduced ungulates (Order: Artiodactyla) in New Zealand. New Zealand Journal of Zoology 29: 323-343.

Gould, S.J. & Vrba, E.S. 1982. Exaptation - a missing term in the science of form. Paleobiology: 4-15.

Greenwood, R.M. & Atkinson, I.A.E. 1977. Evolution of divaricating plants in New Zealand in relation to moa browsing. Proceedings of the New Zealand Ecological Society 24: 21-33.

Hall, E. 2009. A history of Waerenga-o-Kuri. E. Eleanor, Gisborne.

Hett, J.M. & Loucks, O.L. 1976. Age structure models of balsam fir and eastern hemlock. Journal of Ecology 64: 1029-1044.

Hickson, T.W. 1876. Survey of Tawharetoi Block and Reserves, Okahuatiu, Mangatapere, Ahihiroroa, Waikohu - Matawai, Wharekopae Block, traverse of Hangaroa River, Ruakitori River (surveyor's field book). Gisborne, New Zealand.

Howell, C.J.; Kelly, D. & Turnbull, M.H. 2002. Moa ghosts exorcised? New Zealand's divaricate shrubs avoid

photoinhibition. Functional Ecology 16: 232-240.

Janzen, D.H. & Martin, P.S. 1982. Neotropical anachronisms: the fruits the Gomphotheres ate. Science 215: 19-27.

Jones, J.; Gibb, C.E.; Millard, S.C.; Barg, J.J.; Katharine Girvan, M.; Lisa Veit, M.; Friesen, V.L. & Robertson, R.J. 2005. Multiple selection pressures generate adherence to Bergmann's rule in a Neotropical migratory songbird. Journal of Biogeography 32: 1827-1833.

Kelly, D. 1994. Towards a numerical definition for divaricate (interlaced small-leaved) shrubs. New Zealand Journal of Botany 32: 509-518.

Lee, W.G.; Wood, J.R. & Rogers, G.M. 2010. Legacy of avian-dominated plant–herbivore systems in New Zealand. New Zealand Journal of Ecology 34: 28–47.

Lowell, R.B. 1987. Safety factors of tropical versus temperate limpet shells: multiple selection pressures on a single structure. Evolution: 638-650.

Lusk, C.H. 2002. Does photoinhibition avoidance explain divarication in the New Zealand flora? Functional Ecology 16: 858-860.

Lusk, C.H.; Kaneko, T.; Grierson, E. & Clearwater, M.J. 2013. Correlates of tree species sorting along temperature gradients in New Zealand rainforests: seedling functional traits, growth and shade tolerance. Journal of Ecology 101: 1531–1541.

Mark, A. & Baylis, G. 1982. Further studies on the impact of deer on Secretary Island, Fiordland, New Zealand. New Zealand Journal of Ecology 5: 67-75.

McGlone, M.S. & Webb, C.J. 1981. Selective forces influencing the evolution of divaricating plants. New Zealand Journal of Ecology 4: 20-28.

McGlone, M.S.; Richardson, S.J. & Jordan, G.J. 2010. Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes New Zealand Journal of Ecology 34: 137–151.

Pollock, M.L.; Lee, W.G.; Walker, S. & Forrester, G. 2007. Ratite and ungulate preferences for woody New Zealand plants: influence of chemical and physical traits. New Zealand Journal of Ecology 31: 68-78.

Veblen, T.T.; Ashton, D.H. & Schlegel, F.M. 1979. Tree regeneration strategies in a lowland Nothofagus-dominated forest in south-central Chile. Journal of Biogeography 6: 329-340.

Veblen, T.T. & Stewart, G.H. 1980. Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand. New Zealand Journal of Ecology 3: 50-68.

Wardle, P.A. 1985. Environmental influences on the vegetation of New Zealand. New Zealand Journal of Botany 23: 773-788.