Divaricating shrubs in Patagonia and New Zealand

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Abstract: There are at least three hypotheses to account for the abundance of divaricating shrubs in New Zealand: 1) Ratites in the form of 11 species of moa, led to divarication for browse protection (Greenwood and Atkinson, 1977); 2) Divarication evolved as a microclimatic shield (McGlone and Webb, 1981); 3) Divarication evolved to aid leaves in light harvesting (Kelly, 1994). In Patagonia before human arrival, there were browsing mammals in addition to the ratite rhea. To examine the possible influence of the different grazing animals on the degree of divarication in Patagonian shrubs, a transect was established across Argentine Patagonia at c.40° S lat., from Andean forests to the shrub desert of the east, providing a rainfall gradient from 3000mm to 134mm annual precipitation. Divarication Indices of Atkinson (1992), I_{ATK} and Kelly (1994), I_{KEL} were calculated for all shrubs encountered at 20 sites along this gradient. As I_{KEL} gave zero values for four leafless shrubs, including the important *Mulinum spinosum,* this index was not further used for distributional analyses. I_{ATK} gave 18 species as fully divaricate ($I_{ATK} > 14$) and 8 as semi-divaricate ($I_{ATK} <14$). The highest values of I_{ATK} were lower than in New Zealand (Atkinson 1992), a function of a lower number of wide-angle branches (>90º) in Patagonia. All except two species were spiny, as were most other shrubs on the traverse. Unlike the majority of divaricates in New Zealand which retain divarication in dense forest, none of the Patagonian shrubs are divaricate in forest and only two species divaricate in more open forest and scrub. Divaricate cover increased steeply along the traverse through drier, open forest and seral scrub. Once out of the seral scrub zone into arid country, a different suite of divaricate taxa was encountered. The diversity and cover of divaricates rose to reach a maxima at 134 mm annual precipitation. In Patagonia, divarication and spininess could be responses to the indigenous browsing mammals that are common in the semiarid and arid zones, or to climate.

Keywords:, browsing; climate; divarication; mammals; Patagonia; ratite birds.

Introduction

New Zealand's woody flora contains a large proportion of divaricating plants, both as shrubs retaining this form throughout their life, and as the juvenile forms of some trees (Atkinson and Greenwood, 1989). Divaricating shrubs make up 10% of the woody flora, with 50 species (Atkinson and Greenwood, 1989) distributed through all climates and vegetation types, from the most humid forests to semi-arid grasslands. The reason for their abundance and ubiquity has been a matter of conjecture for at least a century. Diels (1897) suggested that the divaricating form is a response to windy and harsh climate during the Pleistocene glaciations. Greenwood and Atkinson (1977) proposed that the divaricating habit is a response to past browsing by the now extinct large flightless ratite birds, the moas. McGlone and Webb (1981) developed Diels' hypothesis that divarication is a response to the wind, frost and abrasion of Pleistocene glacial climates. Kelly (1994) suggested that divarication could also be an aid in light harvesting, due to close packing of leaves at diverse angles.

Definitions of divarication vary (Greenwood and Atkinson, 1977; Tomlinson, 1978; McGlone and Webb, 1981; Halloy, 1990). Kelly (1994) reviews and comments on these definitions:
1. wide-angled branching, often over 90°.
2. interlacing of branches, often consequent on the wide branch angles, but also associated with fastigiate and zigzag branching.
3. density of branching, both as a result of closely spaced lateral meristems and of a relatively high number of branch orders.
4. small leaves, in a range 5-20mm long, as suggested by Tomlinson (1978). Kelly (1994) sets an upper limit to leaf size by area: $< 60mm^2$.
5. long leaf internode length in relation to the leaf size - "filiramulate" (Wardle and McGlone, 1988).

Until recently the lack of an objective definition of "divaricate" has not allowed valid comparisons between different taxa, and with plants in areas outside New
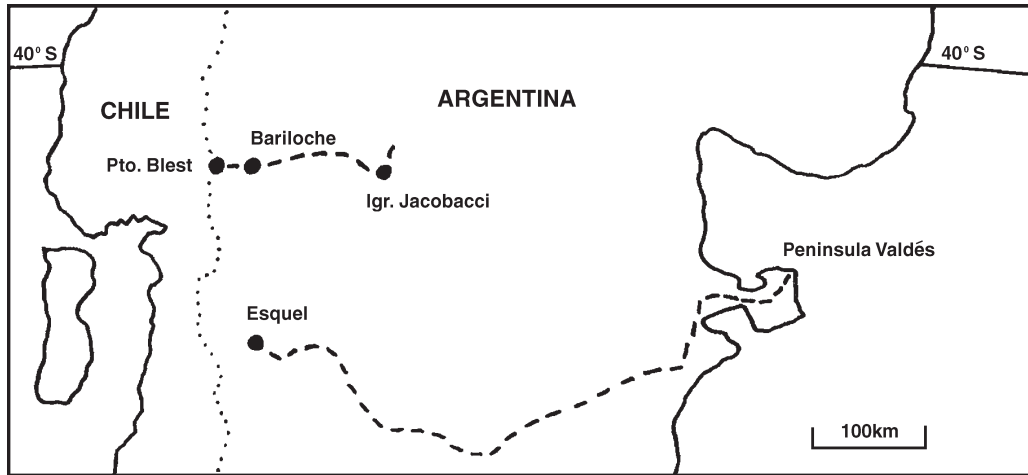
Figure 1. Map of the region of study, showing routes across Patagonia (-------). the northern traverse was by lake (Nahuel Huapi), west of Bariloche and by highway 23 to Ingeniero Jacobacci, then north along highway 6. The southern traverse was on highway 40, to Rawson, highway 3 to Puerto Madryn and local roads to Peninsula Valdés.

Zealand. Atkinson (1992) and Kelly (1994) each attempted to overcome this problem with the development of Divarication Indices (referred to here as I_{ATK} and I_{KEL} respectively) based on measurements quantifying the criteria outlined above.

To gain a new perspective under conditions zoologically different from those in New Zealand, a survey was made in Argentine Patagonia of apparently divaricating shrubs. The biota of Patagonia and New Zealand are quite different. Not only are the plants systematically different, up to the family level but there have been different histories of terrestrial herbivorous animal evolution. In this Patagonia, browsing mammals, as well as one extant ratite bird, Darwin's rhea (*Pterocnemia pennata pennata[1]*) have been part of the pre-human environment. In New Zealand, which completely lacked indigenous terrestrial mammals, the moa, some to 3m high, were the only large vertebrate herbivores. There were 11 species of moa (Cooper *et al.* 1993) before first human contact by Polynesians, who arrived about the 9th century AD. The combined effects of fire, hunting and habitat clearance eventually caused the moa to become extinct about the 16th century. In the 19th century a second wave of human migration, from the Northern Hemisphere, brought a wide range of domestic and feral herbivores. Both areas have similar latitudes and climatic gradients, from superhumid in the west to semi-arid in the east, but reaching arid in Patagonia. Strong dry winds are common in both territories. The present study, based on field work in 1987, sets out to define the degree of

divarication in Patagonia and its geographical variation, from the humid Andean forests in the west to the arid desert scrub in the east. The aims of this paper are: to determine whether the divaricating shrubs seen in Patagonia are architecturally comparable with New Zealand divaricating shrubs; and to describe, quantitatively, the distribution of the Patagonian divaricating shrubs in relation to a west to east precipitation gradient, from superhumid forests to arid deserts.

Methods

Region of Study

The 600 km traverse at 40°-41° S latitude, started in the superhumid forests of the Andes, and progressed through drier forests, seral scrub, tussock grassland (including many areas of *Mulinum spinosum[2]*) into open desert scrub extending to the Atlantic coast (Appendix). The traverse (Fig. 1) was made, mostly by

[1]Nomenclature of birds follows Mayr (1979).

[2]Nomenclature for names of New Zealand plants follow Allan (1961) and Connor and Edgar (1987). Most of the Patagonian plant names and authorities come from Correa (1969-1984) in the incomplete multipart "Flora Patagonica". Names not yet incorporated in this publication came (pers. comm.) from Argentine botanists: Drs. S. Halloy (AgResearch, Dunedin), F.A.Roig (Investigaciones Científícas y Tecnícas, Gobierno de Mendoza, Argentina), Srs Donald Bran (Instituto Nacional de Tecnología Agropecuaria, San Carlos de Bariloche, Argentina) and J. Ambrosetti (Investigaciones Científícas y Tecnícas, Gobierno de Mendoza, Argentina).
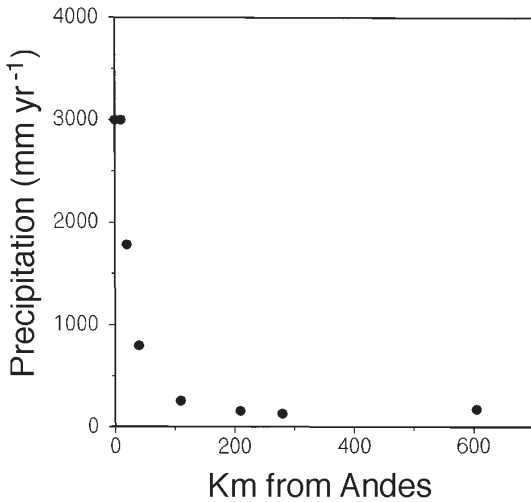
Figure 2. The relation between precipitation and distance eastwards from the Andes.

road, from west to east from Puerto Blest, near the Chilean border with Argentina, to Peninsula Valdés, on the Atlantic coast of Argentina.

Along this traverse, annual precipitation generally decreases from 3 000 mm in the west to 169 mm on the Atlantic coast (Appendix). The precipitation gradient is especially steep in the first 80 km of the traverse (Fig. 2). This gradient is an expression of the rain shadow effect of the Andes, similar but more extreme to that that occurs across the South Island of New Zealand. As in New Zealand, föhn westerly winds elevate the temperature and lower the precipitation and humidity east of the Andes.

Sampling was done in a range of vegetation types (Fig. 3 and Appendix). In the west are Andean superhumid forests (3000 mm annual precipitation, 900 m altitude). These mixed evergreen forests are dominated by *Nothofagus dombeyi* with emergent *Saxegoethea conspicua* and *Fitzroya cupressoides*, with abundant bamboo (*Chusquea* spp.). At higher altitudes, up to 1400 m are subalpine *Nothofagus pumilio*
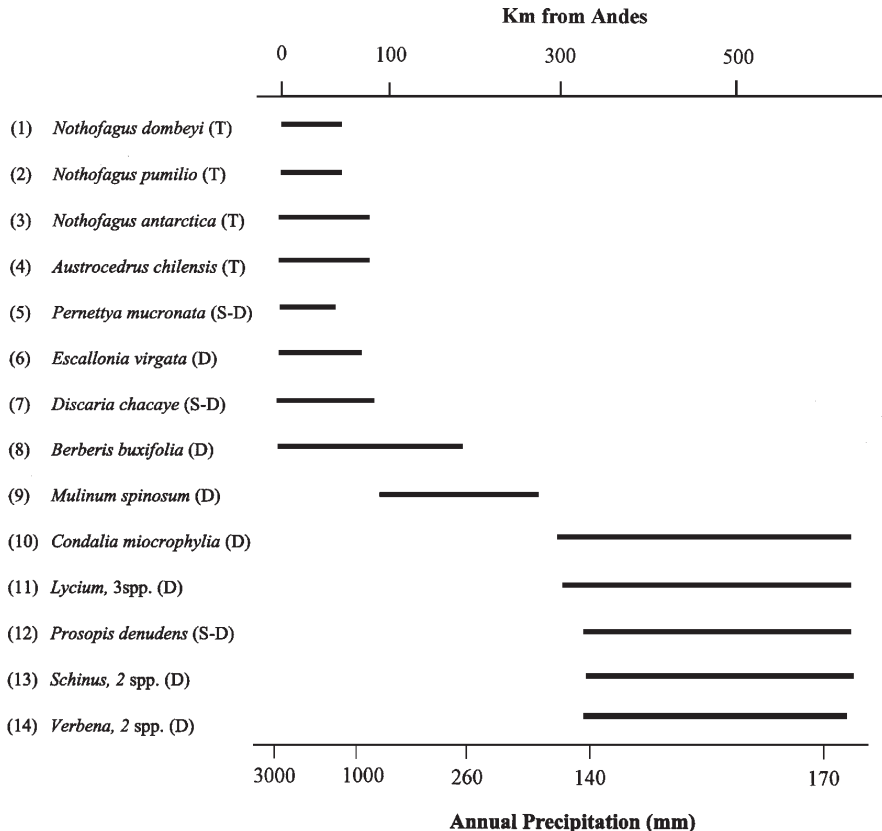
Figure 3. Diagram from the traverse of Patagonia of the ranges of main forest dominants (the upper four) and dominant taxa of shrubs examined for divarication Indices in the present study. (T) = Tree, (D)= Divaricating, $I_{ATK} > 14$. (S-D) = Semi Divaricating, $I_{ATK} < 14$.

forests with estimated precipitation of 3000mm annually. To the east are drier (1800-1200mm precipitation), pure *N. dombeyi* forests, but still with bamboo. Within these forests frost hollows and mires carry the shorter, deciduous *N. antarctica*, also found on burn seres. This species, along with *Austrocedrus chilensis* forms a fire-fragmented zone of steady-state scrub and forest in areas above 800mm annual precipitation. This scrub and forest merges eastward into pre-Andean seral scrub. Within the present forest areas, but especially to the east of existing forests, seral scrub has developed in the last 100 years (Veblen and Lorenz, 1988; Veblen *et al.*, 1992). This scrub is on sites of former forests, burnt by indigenous people up to the late 19th century. This phase was followed by a lowered fire intensity associated with European domestic stock, and consequent overgrazing and impedance of tree regeneration. Eastwards of this scrub zone is tussock grassland, much of it replaced after overgrazing by *Mulinum* steppe (Léon and Aguier, 1985). This steppe in turn merges eastwards into the arid desert scrub.

In this study, the majority of forest samples were taken at 900-1100m altitude in valleys or on the lower sedimentary hills east of the Andes (Appendix). In addition, some sampling was done in subalpine deciduous *Nothofagus pumilio* forests at 1400-1500m at or near the treeline, on mid to upper slopes. Beyond the forest, seral scrub zone and tussock-*Mulinum* zone, all at c.900m altitude, the desert scrub was sampled at altitudes dropping from 800m to 80m over a distance of 400km.

Browsing Animals

Patagonian vegetation has evolved with large browsing mammals present before humans arrived in the Holocene. Late Pleistocene extinctions (Markgraf, 1985) include a horse (*Onohippidium*) and a camelid (*Lama gracilis*[3]). The giant ground sloth (*Mylodon*) that became extinct in the early Holocene was a herbivore well adapted to Pleistocene arid conditions, its faeces having yielded pollen of Poaceae and Chenopodiaceae, then dominant over much of Patagonia. Despite its size, *Mylodon* was on this evidence a browser of herbs, not larger shrubs and small trees.

Indigenous animals observed today are: in forests, the small Cervid huemul (*Hippocamalus bisulcus*) while in more open country there are occasional guanaco (*Lama guanicoe*) and Darwin's rhea, (*P. pennata pennata*). The two latter large herbivores are abundant only in the wildlife reserve of Peninsula Valdés, sharing the scanty vegetation with farmed merino sheep (*Ovis aries*). Mainwaring (1983) gives an account of the massive slaughter of guanaco and both species of rhea in the early days of sheep farming, around the end of the 19th century.

The frequency of road kills of mara (*Dolichotis patagonum*), suggests that this hare-sized rodent is still common. A subterranean rodent, the root-eating tucu-tucu (*Ctenomys* sp.) is localised in sandier soils. Introduced sheep, cattle, horses and goats are present in all vegetation except the most inaccessible, densely forested parts of National Parks near the Chilean border.

Site Descriptions

At each of the 20 sites, a brief description of vegetation was made by compiling species lists with a visual estimates made of canopy cover. The community dominants are listed in the Appendix I which also records the presence of spininess on all non-divaricating shrubs, expressed as number of species of spiny shrubs per plot.

Plant Characters Measured

The field work was done before the publication of the divarication indices of Atkinson (1992) and Kelly (1994). A series of measurements, including most of those later used by Atkinson (1992) and Kelly (1994) were suggested to me in 1986 by S. Halloy (AgResearch, Dunedin, New Zealand, *pers. comm.*). These measurements were taken on individual specimens at each location to avoid confusion in species, mostly unknown, at the time of field work. The following measurements were taken on the parts of plants not directly exposed to the very strong westerly winds, within a light metal cubic frame of 30cm internal sides in the 10 cm deep peripheral zone of each plant:
– leaf width and length, from 5 peripheral leaves
– density of branches at > 70° along the chosen 10 cm axis
– number of branch orders

The number of branch angles > 90° and the mean angle of branching, not included in Halloy's list of field measurements were subsequently estimated in New Zealand from large projections of close-up colour slides of the shrubs. The presence in each photograph of the cubical metal frame allowed reasonable rectification of planes of angle measurement.

Leaf size data were also collated for 21 New Zealand species either from field measurements used by Kelly (1994) and provided by him (Dave Kelly, University of Canterbury, Christchurch, New Zealand, *pers. comm.*) or measured from field and open cultivated specimens. A few were from herbarium specimens, taken with care to avoid linear leaves that had rolled up in drying.

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[3]Nomenclature for mammals follows Gibb and Flux (1973) and Honacki *et al.* (1982).

Divarication Indices

Shrubs which appeared to be divaricating were scored for Atkinson's (1992) index - I_{ATK}, and where possible for Kelly's (1994) alternative index - I_{KEL}. Among the Patagonian shrubs studied, several were leafless plants: *Bredermeyera colletioides*, *Mulinum spinosum*, *Parastrephia* sp. and *Verbena thymifolia* (despite its name, the minute leaves were closely imbricated and adpressed to the stem so the stem was in effect a smooth photosynthetic organ). These four species had to be omitted from calculation of I_{KEL}.

Results

Divarication in Patagonian shrubs
Divaricating shrubs are frequent in Patagonia (Table 1). Two groups may be recognised:

(1) semi-divaricating shrubs with I_{ATK} <14. There are 9 Patagonian shrubs in this class.
(2) Patagonian shrubs with I_{ATK} > 14. There are 19 shrubs in this class which fall within Atkinson's definition of true divaricates. The highest value recorded in Patagonia is I_{ATK} = 23.4 for *Schinus fasciculatus*. New Zealand values frequently exceed this; six species recorded by Atkinson (1992) had values greater than 23.4 and reached a high of 36.6 for *Coprosma virescens*. Another high scoring Patagonian plant is *Mulinum spinosum*, at I_{ATK} = 22.2. This plant (Figure 4) has no wide angle branches, and is a virtually leafless, hemispherical, suffruticose plant, dying back annually to a root stock. Its high divarication index is caused by extremely dense terminal branching, giving it a form like some alpine *Aciphylla*, in the same family (Apiaceae).

Table 1. Semi-divaricating and divaricating species from Patagonia, with data used to calculate the Divarication Index(I_{ATK}) of Atkinson, (1992) and Kelly (1994) I_{KEL}. Kelly (1994) gives I_{KEL}=19.2 as a lower limit of divarication on New Zealand examples. Species are ranked in order of ascending I_{ATK}.

	Plot (see Appendix)	Peripheral wide-angle branches	Mean branch angle/10 n=10	No. branch orders	Branching density /10cm, n=5	Leaves /10cm	Leaf length mm n=5	Leaf width mm n=5	I_{ATK}	I_{KEL}
Semi-divaricating species (I_{ATK} <14)										
Discaria chacaye	16	1	5.6	2	1.2	25.0	13.2	5.0	9.8	14.0
Berberis heterophylla	16	0	5.8	3	1.8	26.8	13.2	4.8	10.6	14.5
Senecio filaginoides	15	0	4.8	2	4.6	34.2	15.6	2.4	11.4	15.0
Tetraglochin alatum	15	0	4.2	3	4.2	19.8	4.0	2.2	11.4	15.3
Bredermeyera cf. Colletioides	1	2	7.1	2	1.5	Leafless			12.6	
Prosopis denudens	3	0	6.2	3	3.5	12.4	5.4	1.0	12.7	30.5[1]
Adesmia campestris	11	1	5.4	3	5.0	10.0	4.8	1.1	13.4	29.0[1]
Pernettya mucronata	19	0	5.7	2	6.0	30.0	12.0	7.0	13.7	13.3
Parastrephia sp.	13	0	5.6	3	5.1	Leafless			13.7	
True divaricating species (I_{ATK} >14)										
Bougainvillea spinosa	2	4	5.0	3	2.5	34.0	6.2	1.0	14.5	27.9
Compositae (unidentified)	3	0	4.3	4	7.2	15.6	4.8	1.0	15.5	25.1
Condalia microphylla	1	0	7.0	3	5.4	25.0	4.8	1.7	15.5	22.2
Atriplex lampa	12	0	3.4	4	8.6	41.2	9.8	2.0	16.0[1]	13.0
Escallonia virgata	16	1	7.4	3	4.7	25.0	12.5	5.0	16.1[1]	17.6
Verbena aff. Aspera	13	3	6.8	3	3.3	21.2	13.4	3.4	16.1[1]	17.7
Lycium chilense	12, 13	1	5.0	3.5	7.7	74.0	6.6	1.6	16.2[1]	17.1
Verbena thymifolia	2	0	7.8	3	5.6	Leafless			16.4	
Acantholippia seriphioides	13	2	7.3	3	4.4	77.0	1.3	1.0	16.7	25.8
Verbena sp.	4	0	7.4	3	6.4	34.4	4.4	1.0	16.8	27.6
Maytenus chubutensis	19	2	5.9	3	6.0	20.0	1.0	6.0	16.9[1]	14.3
Lycium sp	2	0	7.6	3	7.8	39.6	4.6	1.0	18.4	27.2
Berberis buxifolia	9	4	8.2	3	3.7	23.6	21.8	5.4	18.9[1]	19.0
Lycium gilliesianum	4	5	6.3	4	3.8	64.0	17.6	2.1	19.1[1]	18.1
Lycium ameghinoi	12	3	7.6	3	6.9	51.0	10.0	3.6	20.5[1]	18.4
Mulinum spinosum	9	0	7.2	2	13.0	Leafless			22.2	
Schinus johnstonii	1	5	5.6	4	8.4	19.8	5.8	4.6	23.0[1]	14.5
Schinus fasciculatus	1	4	7.0	4	8.4	24.4	14.0	14.0	23.4[1]	15.0

[1]Species which are classified as divaricate on one index and not the other

Table 2. Average leaf dimensions for Patagonian and New Zealand semi-divaricate (I_{ATK} < 14) and fully divaricate (I_{ATK} >14) shrubs.

Divarication	Leaf Length mm		Leaf Width mm	
Index (I_{ATK})	<14	>14	<14	>14
Patagonia				
Mean (S.E.)	9.4 (2.1)	9.4 (1.3)	2.8 (0.7)	3.0 (0.5)
Range	4.0-15.6	1.3-21.3	1.0-5.0	1.0-7.0
n	6	17	6	17
New Zealand				
Mean (S.E.)	8.1 (1.6)	7.5 (0.6)	5.0 (1.1)	3.8 (0.5)
Range	2.6-14.4	2.2-14.8	1.0-11.8	0.7-10.8
N	8	33	8	33
Comparison				
t	0.493	1.505	1.290	0.938
P	0.631	0.139	0.221	0.353

Patagonian shrubs generally had few wide angled (>90°) branches compared to the New Zealand divaricates (Patagonia average 1.89, n = 18; New Zealand average 4.96, n = 24; $t = 4.60$ P <0.0001). As a consequence, most New Zealand divaricates have a tendency, not matched in the Patagonian shrubs, for the peripheral branches to interlace and form a sort of shield.

Leaf size in Patagonian and New Zealand divaricates

There were no significant differences between Patagonian and New Zealand divaricates in leaf length or leaf width (Table 2). Thus, variation in leaf size does not appear to be associated with the difference between semi-divaricates (I_{ATK}<14) and true divaricates (I_{ATK} >14). This applies equally in Patagonia and New Zealand. Patagonian plants tend to have longer, narrower leaves. Apart from the one exception (*Berberis buxifolia* of mean length 21.8 mm), leaves of all other Patagonian divaricates are less than 20mm in length, thus satisfying one of Tomlinson's (1978) criteria of divarication.

Spininess of shrubs

Of the 17 true divaricates (I_{ATK} >14) studied in Patagonia, only two were not spiny. These were *Maytenus chubutensis* and *Escallonia virgata*, both found in the higher precipitation part of the traverse (600-3000mm annually). *Escallonia virgata* has highly aromatic leaves, possibly repulsive to animals. *Maytenus chubutenis* had no smell, but was never seen nibbled. The spininess of the other divaricates suggests protection against browsers.

Other non-divaricating shrubs in the higher precipitation areas were spiny, notably *Discaria* spp.,
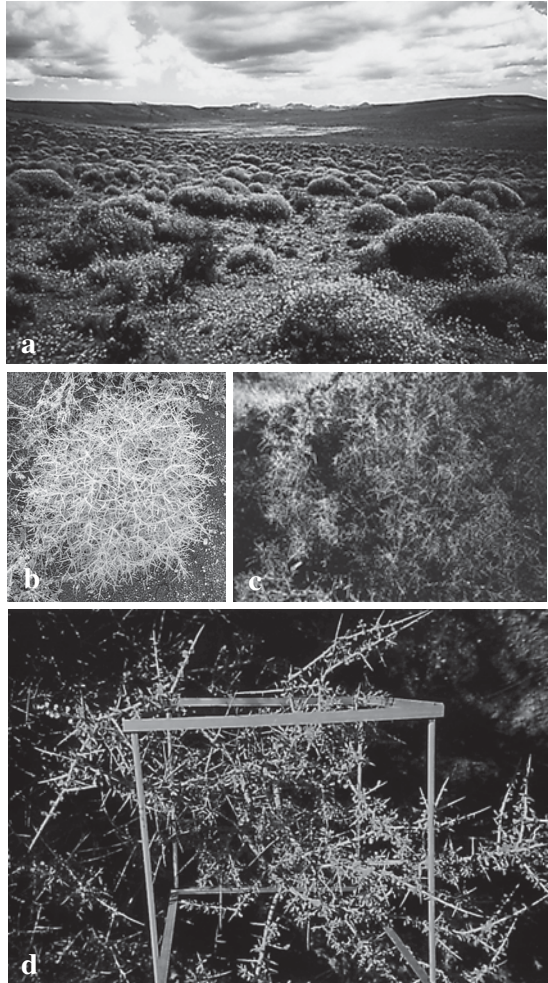
Figure 4. (a) *Mulinum spinosum* landscape north of Norquinco, Rio Negro, photo by Pamela Searell; (b) *Mulinum spinosum* near Bariloche - this leafless divaricate has I_{ATK} of 22.2, photo by Alastair Robertson; (c) *Lycium* sp., 200km east of the Andes. Probably campfire scorching has exposed the branch divarication clearly - this species has I_{ATK} of 18.4, photo by Ross McQueen; (d) *Schinus johnstonii* near the Atlantic coast - I_{ATK} is 23. The metal frame has 30cm internal dimensions on each side, photo by Ross McQueen.

Berberis spp. and the bamboo, *Chusquea*. In the arid areas *Chuquiraga*, *Nassauvia* and Cactaceae were spiny. Across the traverse of Patagonia, there was little variation in the number of spiny shrub species encountered. In a range of 0-3 species per sample and a mean of 2 , the correlation coefficient of number of spiny shrubs with distance from the Andes was r =0.082, n = 21, not significant at P=0.05.

Table 3. Families having species which are fully ($I_{ATK} > 14$) and semi- divaricating ($I_{ATK} < 14$) in Patagonia and the occurrence of those families in New Zealand.

Family	New Zealand[1]	Patagonia
Rhamnaceae	Yes	*Discaria, Condalia*
Leguminoseae	Yes	*Adesmia , Prosopis*
Ericaceae	No	*Pernettya*
Anacardiaceae	No (Is.)	*Schinus*
Chenopodiaceae	No	*Atriplex*
Compositae	No	*Parastrephia, Senecio* and 1 unid.
Escalloniaceae	No	*Escallonia*
Nyctaginaceae	No (Is.)	*Bougainvillea*
Rosaceae	No	*Tetraglochin*
Solanaceae	No	*Lycium*
Umbelliferae	No	*Mulinum*
Verbenaceae	No	*Acantholippia, Verbena*
Berberidaceae	absent	*Berberis*
Celastraceae	absent	*Maytenus*
Polygalaceae	absent	*Bredermeyera*

[1]Yes = divaricating in New Zealand; No = non-divaricating in New Zealand, with Patagonian representatives showing full or semi-divarication. Is. = present only on outlying northern islands of New Zealand.

Comparison of divarication indices

Kelly (1992) tested his and Atkinson's Indices for correlation. His best result, for 19 New Zealand species, was $r = 0.66$, $P = 0.002$. For the 23 leaf-bearing Patagonian species (Table 1) there was no significant correlation ($r = 0.004$) suggesting that the two indices measure different aspects of plant architecture that are correlated in New Zealand plants but not in Patagonian divaricates. The four leafless Patagonian species could not be included in this analysis. Of the remaining 23 species, two were classified as divaricates on I_{KEL} but not on I_{ATK}, and ten that were classified as divaricate on I_{ATK} but not on I_{KEL}.

There are many southern genera in common between New Zealand and Chile (Godley, 1961), noticeably *Nothofagus*, *Podocarpus*, *Cortaderia* and *Gunnera*. However, among plants tending to divarication east of the Andes, only two genera are in common: *Discaria* and *Pernettya*, (both $I_{ATK} < 14$) (Table 3). These systematic data are evidence that divarication is not a character embedded deeply in the evolutionary history of these plants, but rather a character evolved in response to local conditions. While divaricates are common in New Zealand forests, in Patagonia divaricates are only found in open country.

Divaricating shrub distribution from west to east across Patagonia

The number of divaricating species in Patagonia increase with distance from the Andes and decreasing
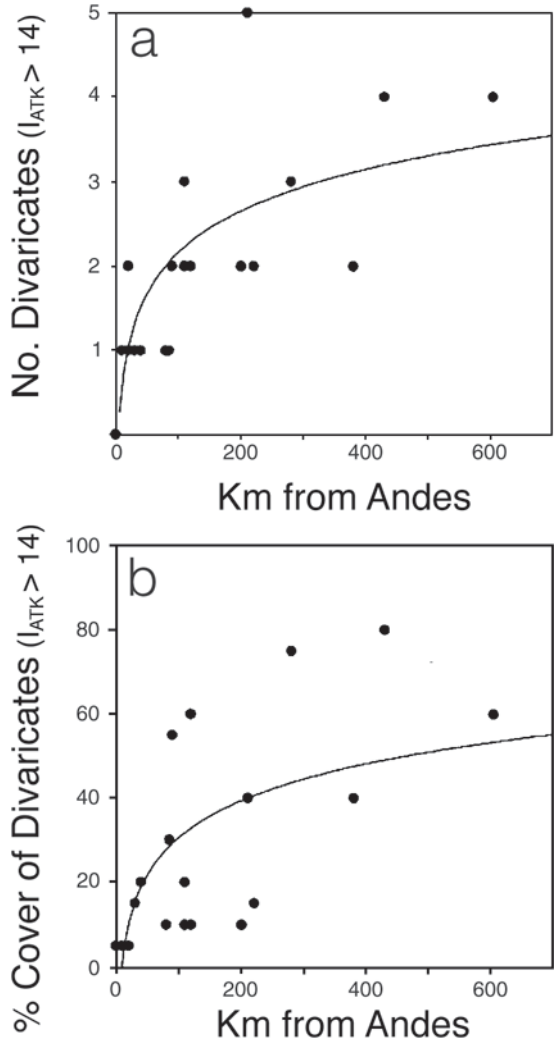
Figure 5. (a) Relationship between number of true divaricate shrubs ($I_{ATK} > 14$) and distance eastwards from the Andes ($r = 0.747$, $P = < 0.001$, $n = 20$, $y = 1.639\log(km) - 1.170$). The eastern forest boundary is at approximately 40 km along the transect. (b) Relationship between cover of true divaricate shrubs ($I_{ATK} > 14$) and distance eastwards from the Andes ($r = 0.662$, $P = < 0.01$, $n = 20$, $y = 29.39 \log(km) - 28.36$).

precipitation from none in the wettest forest zone, through two in more eastward forests, to four in the most arid areas (Figure 5a). This maximum is reached at the edge of the arid zone, eastwards of 200 km from the Andes. Percentage cover of divaricates showed a similar trend (Figure 5b). However the average values of divarication, (I_{ATK} and I_{KEL}), showed no similar correlation with distance from the Andes.

There were no divaricating shrubs in the wetter and denser mixed forests at the Chilean border at 900m altitude, nor in the subalpine forests of *Nothofagus pumilio* at 1500m in the same area. There were two species, *Maytenus chubutensis* and *Berberis darwinii,* that were divaricate in more open conditions but lax in these forests*,* and another lax species, *Pernettya mucronata,* that became close to divarication (I_{ATK}=13.7) under open conditions. These three species only showed divarication in these meso-sites, and were noted as lax in more closed situations. Similarly, the Chilean and Argentinian *Berberis darwinii*, naturalised in New Zealand is also very lax, almost lianoid under a dense low forest canopy, but divaricating out in the open (McQueen, 1993). It was not encountered in open conditions on the present survey, but straggling, lianoid plants were seen in Andean forests.

The forest canopies are noticeably more open towards the east of the forested zone. However, no correlation was found at individual plots between the estimated canopy cover and diversity or cover of divaricating shrubs.

Discussion

The results presented show that there are divaricating shrubs in Patagonian Argentina as measured by Atkinson's (1992) divarication index. In a west-east traverse of 600km their presence and cover increase along a gradient of decreasing precipitation. Divaricating shrubs are absent from the wettest forests then increase in cover into the drier forests, seral scrub, and *Mulinum*/grass communities, and peak in the arid desert scrub.

Patagonian true divaricates ranged from I_{ATK} 14.5 to 23.4 compared to a range of 14 to 36.6 given by Atkinson (1992) for New Zealand true divaricates. The lower values from Patagonia appears to be due to the significantly lower number of peripheral branches at > 90° (wide-angle branches). Although branches at about 60°-80° are common on many Patagonian shrubs, the scarcity of wide angle branches of 90° or over means that there is less interlacing and less likelihood of the formation of an external "shield" of interlaced branches.

Kelly (1994) has also suggested a divarication index that is based, in part, on leaf size. The four leafless Patagonian species had, by necessity, to be excluded. On this index, only nine Patagonian species were divaricate. For New Zealand plants Kelly (1994) records a high and significant positive correlation between I_{ATK} and I_{KEL} for 19 species. In Patagonia, there was overall no significant correlation between the two indices for all species tested by both indices.

This lack of consistency lies in the different characteristics the two indices emphasise. Atkinson's I_{ATK} is made up of four plant "framework" parameters derived from branching pattern - branch angle and order, the number of widely diverging angles and the density of branching. In contrast, I_{KEL} is more concerned with leaf size and shape and the degree of leaf spacing. That the two indices correlate in New Zealand and not in Patagonia suggests that they describe separate aspects of the divaricating habitat that are coupled in New Zealand but not in Patagonia. Thus 10 of the Patagonian plants had diverging branch angles but not small spaced leaves and two had small leaves but not the strongly diverging branches.

Reasons for divarication

The formation of a shield of peripheral branches in New Zealand has been interpreted as a means for protection of the plant against some unfavourable aspect of the environment. This protection could be against herbivore browsing (Greenwood and Atkinson, 1977; Atkinson and Greenwood 1989) or could equally be against harsh climatic conditions (McGlone and Webb, 1981).

Of the divaricates examined in Patagonia, all except two (*Maytenus chubutensis* and *Escallonia virgata)* are spiny while in New Zealand divaricating shrubs, only *Discaria toumatou*, is spiny. Such a difference also suggests that the spininess of Patagonian divaricates and of many other shrubs is a response there to co-evolution with mammals. The two non-spiny Patagonian species are apparently non-palatable and are plants of the Andean forest and adjacent seral scrub. The spininess of all other divaricates, and of many non-divaricates in Patagonia may be associated with the natural presence of soft-lipped mammals in the South American sector of Gondwanaland.

Daciuk (1978) identified, from direct observation and examination of stomach contents, the plants ingested by the ratite, Darwin's rhea, at Peninsula Valdés, at the Atlantic end of the traverse described in the present paper. Here, divaricating shrubs are common in the desert scrub. Daciuk found that Darwin's rhea eats grasses and herbs, often scratching with its claws into the soil for underground plant parts. Food obtained above ground included the flowers of Asteraceae, some from spiny plants, and the fruits of two divaricates (*Condalia microphylla* and *Lycium chilense*). Leaves and stems of succulent plants, including *Opuntia* were also eaten. Daciuk did not find gastroliths in any dissected rhea, a finding consistent with a diet of softer plant parts.

Pelliza-Sbriller *et al.* (1983), studied the diet of Patagonian wild and domestic herbivores from faecal cuticular remains. This study was at Pilcaniyeu, 120 km from the Andes, in an area dominated by *Mulinum spinosum* and the spiny *Nassauvia glomerulosa*. Sra. Pelliza-Sbriller (Instituto Nacional de Tecnología

Agropecuaria, San Carlos de Bariloche, Argentina, *pers. comm.*) stated that it was not possible, on cuticular evidence, to determine which parts of plants were ingested. In January *Mulinum spinosum* dominated the food of Darwin's rhea. It is likely that it was the seeds that were eaten, as personal observations on this very densely spined plant showed no sign of stem browsing. Grasses and herbs made up the rest of the summer food. By April, when *Mulinum spinosum* died back to a root stock, it formed a very small part of the rhea's diet, and the herb *Perezia* dominated the rhea's diet. The accounts of Daciuk (1978) and Pelliza-Sbriller (1983) give the impression of a bird whose beak, flat in cross section, does not cut, but rather plucks accessible parts of plants. It is possible that the beak is an advantage in penetrating slightly into spiny divaricates (*Condalia* and *Lycium*) to eat the fruits.

The very similar, more northern Patagonian *Rhea americana*[4] was observed by the author in two zoological parks. In the first (Honolulu), lettuce leaves on the ground were tossed by the rhea until they broke, then swallowed. Likewise in Wellington, New Zealand the leaves on cut willow branches were tugged and shaken until the leaves came off. This second situation may have been more analogous to natural conditions as the willow branches, quite weighty, were similar to a rooted plant.

The eating habits of rhea are unlike those surmised for some of the larger extinct New Zealand moa (*Dinornis* spp.) which could cut twigs to 5mm diameter (Burrows *et al.*, 1981). The sub-fossil gizzard samples studied by them included some very fibrous stems (*Plagianthus*, *Muehlenbeckia*), impossible to break by hand. The combination in the moa of a strong shearing beak (Atkinson and Greenwood,1989), and gastroliths suited this ratite to a diet including lignified material. The rhea, with a flat plucking beak, and no gastroliths has been shown here to be adapted to a softer diet. The rhea, outweighed in diversity by browsing mammals appears to be only a minor contributor to any divaricating adaptations in Patagonia.

Climate and divarication

The increase in both diversity of divaricating species and their cover, along a gradient of decreasing precipitation, could be interpreted as a direct effect of decreasing precipitation, but there are other potentially confounding factors. The forests near the Andes have mixed canopy heights and a dark floor. The forest canopies become monotypic and noticeably more open to the east of the Andes. This openness may account for the eastwards increase in cover of divaricates. The openness may be due to decreased precipitation and

simple structure, but may also be related to human exploitation. Random felling of isolated trees allows either the invasion by the bamboo, *Chusquea*, a strong deterrent to forest regeneration (Veblen and Ashton, 1978), or encourages grazing by free range domestic stock.

It has been suggested, without data (McGlone and Webb, 1981) that the tight exterior of New Zealand divaricates is, among other protections, a shield developed in the Pleistocene against sand abrasion and frost. However, microclimatic experiments by Kelly and Ogle (1990) showed little difference between external and internal temperatures and humidity of two New Zealand divaricates. If divarication were a protection against harsh climate one would expect the Patagonian divaricates to show a form of external shield similar to some New Zealand divaricates. Today's windy Patagonian climate, and large areas of bare substrate, encourage the movement of abrasive mineral particles. In fact only one species of Patagonian divaricate, *Mulinum spinosum*, forms a tightly covered hemispherical shape. But *Mulinum spinosum* does not grow in the really arid vegetation of Patagonia, but only in areas between c 800 and 250mm annual precipitation.

Kelly (1994) suggests that divarication may also be a mechanism useful in light-harvesting, by the varying leaf angles and close packing of them on divaricate shrubs. This could be advantageous for divaricates under forest canopies, a common occurrence in New Zealand. In this respect the shrub, *Teucrium fruticans* (Labiatae), introduced in New Zealand, shows strong similarity to divaricates in its branch architecture. It is not a rigid plant, has leaves well over 20 mm long but could form the basis for experimental testing of this light-harvesting hypothesis.

Conclusion

The factors associated with divarication are multiple. In Patagonia, divarication, with spininess, could have evolved in the early Tertiary in the company of browsing mammals. The ecoclimate had already differentiated, by Andean orogeny, into wetter forested west and drier steppes to the east, by the end of the Oligocene, 24 my BP (Romero,1978). A similar differentiation was not complete in New Zealand until the Pliocene, 5my BP, although in the late Miocene, 10 my BP, eastern forests showed characters of lower rainfall (Mildenhall and Pocknall,1984).

Cooper *et al.* (1993) suggest, on molecular evidence, the existence of moa since the separation of New Zealand at c. 80 my BP. In the predominantly forested environment before the Pleistocene, divarication could have developed in shrubs and juvenile trees in forest environments, as protection against moa browsing. The majority of forest divaricates in New Zealand retain this form in the shade, a complete

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[4] Darwin (1860) only apprecated the difference in the two species of rhea when eating parts of a Darwin's rhea.

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Table 4. Numbers of divaricate shrubs (I_{ATK} >14) in different vegetation types in New Zealand and Patagonia. The New Zealand data, for the whole country, come from graphs in Atkinson and Greenwood (1989), the Patagonian data from the limited amount collected in another reconnaissance traverse across Argentina (Figure 1).

	Forest	Scrub and shrubland	Grassland and open
New Zealand	33	51	22
Patagonia	0	13	3

contrast to their laxity in Patagonian forests. This reasoning reinforces the original hypothesis of Greenwood and Atkinson, (1977) that moa played a dominant role in selection of divarication in woody plants.

Before human arrival, in the eighth century A.D., most of New Zealand was forested up to the alpine treeline. Of the total of 53 divaricates, 33 are listed as capable of growth in forests (Table 4). With reduction of forest area after human occupation, it is conceivable that those divaricates surviving or establishing on old forest sites did so with their architecture an advantage in more exposed conditions. The divaricates found today in New Zealand's limited semi-arid areas, not naturally forested, may have evolved to this form as a result of moa browsing and, like the divaricates of the arid areas of Patagonia, are therefore able to grow in harsh conditions.

Acknowledgements

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Appendix. Localities sampled for divaricating shrubs in a traverse across Argentine Patagonia (Fig. 1) Distance from the Andes, at the Chilean border are straight line.

Plot No	Km from Andes	Altitude m	Vegetation	Locality[1]	Province	Pptn/yr mm
D19	0	900	Andean *Nothofagus dombeyi* forest	Puerto Blest	Rio Negro	3000[4]
D21	10	1500	Subalpine forest *Nothofagus pumilio*	Paso Puyuhue	Neuquen	c. 3000 est[4]
D7	20	1100	*Eastern N. dombeyi* forest	Villa la Angostura	Neuquen	1783[2]
D8	20	900	*N. antarctica* forest (seral)	Villa la Angostura	Neuquen	
D18	30	1500	Subalpine forest *Nothofagus pumilio*	Cerro Lopez	Rio Negro	
D17	40	800	*N. antarctica* open forest	5 km S. of Brazo Huemul, L. Nahuel Huapi	Neuquen	800[3]
D6	80	900	*Berberis/Mulinum/Stipa* shrubland/grassland	10 km W. of Tecka (RN25)	Chubut	
D16	85	900	*Berberis - Discaria* scrub (semi arid)	5 km W. of Perito Moreno Railway Stn (RN23)	Rio Negro	
D9	90	900	*Berberis/Nassauvia-Mulinum* scrub	10 km W. of Pilcaniyeu Viejo (RN23)	Rio Negro	
D10	110	950	*Mulinum - Nassauvia - Stipa - Festuca* shrub/grassland	INTA farm. Pilcaniyeu Viejo (RN23)	Rio Negro	257[2]
D11	110	950	*Berberis - Adesmia/Mulinum - Stillingia/Stipa* Shrub/grassland	INTA farm. Pilcaniyeu Viejo (RN23)	Rio Negro	
D14	120	900	*Colliquaja - Lycium/Mulinum* scrub	5 km E of INTA farm Pilcaniyeu Viejo (RN23)	Rio Negro	
D15	120	900	*Colliquaja/Mulinum - Anarthrophyllum* low scrub	5 km E of INTA farm Pilcaniyeu Viejo (RN23)	Rio Negro	
D12	200	800	*Atriplex - Lycium/Chuquiraga* scrub	20 km N. of Ingeniero Jacobacci (RP 6)	Rio Negro	
D13	210	900	*Acantholippia - Prosopis -Verbena* Shrubland	60 km N. of Ingeniero Jacobacci (RP 6)	Rio Negro	158[3]
D5	220	800	*Adesmia/Nassauvia* scrub	21 km W. of Paso de Indios (RN 25)	Rio Negro	
D4	280	300	*Schinus - Lycium/Stipa* scrub grassland	4 km E. of ACA service stn. Valle de los Altares(RN 25)	Rio Negro	134[3]
D3	380	200	*Prosopis - Lycium/Chuquiraga* scrub	10 km W. of Alto de las Plumas (RN 25)	Rio Negro	
D2	430	100	*Chuquiraga - Atriplex-Verbena* scrubland	4 km N. of Digue Florento Ameghino RN 25	Rio Negro	
D1	605	80	*Schinus/Chuquiraga* scrub	5 km W. of Park H.Q. Peninsula Valdes(RP 2)	Rio Negro	169[3]

[1] Road Designations: RN = Ruta Nacional; RP = Ruta Provincial
[2] Rainfall data obtained from *Sr. Arrigo Marcolin, INTA, San Carlos de Bariloche, Pcia. Rio Negro*
[3] Rainfall data obtained from Anon.(1958)
[4] Rainfall data obtained from Rabasso *et al.* (1981)