120 years of untangling the divaricate habit: a review

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The evolution of divaricate plants in New Zealand has been the subject of long-running debate among botanists and ecologists. Hypotheses about this remarkable case of convergent evolution have focused mainly on two different types of selective pressures: the Plio-Pleistocene advent of cool, dry climates, or browsing by now-extinct moa. Here, we review the scientific literature relating to New Zealand divaricates, and present a list of 81 taxa whose architectures fall on the divaricate habit spectrum. We recommend a series of standardised terms to facilitate clear communication about these species. We identify potentially informative areas of research yet to be explored, such as the genetics underlying the establishment and control of this habit. We also review work about similar plants overseas, proposing a list of 53 such species as a first step towards more comprehensive inventories; these may motivate further studies of the ecology, morphology and evolutionary history of these overseas plants which could help shed light on the evolution of their New Zealand counterparts. Finally, we compile published divergence dates between divaricate species and their non-divaricate relatives, which suggest that the divaricate habit is fairly recent (< 10 My) in most cases.

Introduction

The earliest mention we have found of what we call today "divaricating plants" or "divaricates" was made in 1896 by German botanist Ludwig Diels. He described them as "systematically distant descendants of the New Zealand forest flora that converged towards a xerophytic structure" (Diels 1896, pp. 246-247, translated from German). He expressed surprise at seeing apparently drought-adapted species in climates that are generally more humid than in his native Central Europe, where plants do not show similar architectures. These plants are nowadays recognised as a collection of shrubs and early growth stages of heteroblastic trees bearing small leaves on tangled branches diverging at wide angles.

Such a case of convergent evolution naturally attracted much attention from local and overseas botanists and ecologists. The centre of this attention was to identify putative selective forces that may have driven this evolution. Diels (1896) initially proposed drought as the main selective factor,

and McGlone & Webb (1981) considered that frost and wind might also have been important. Diels' climatic hypothesis remained largely unchallenged until Greenwood & Atkinson (1977) developed the moa-browsing hypothesis that several authors had previously hinted at (e.g. Denny 1964; Carlquist 1974; Taylor 1975), igniting a passionate debate that is still ongoing today. Concurrently, a non-selective evolution process was proposed by Went (1971): the horizontal transfer of "divaricate" genes; it however was strongly criticised on theoretical grounds (Tucker 1974; Greenwood & Atkinson 1977) and has not been empirically investigated so far.

Rationale for and content of this review

Although about 120 years have passed since the first publications on the topic, the real debate around the evolution of divaricates only started in the late 1970s. Yet, no recent literature review (e.g. Wilson & Lee 2012) offers an exhaustive account of all the scientific material published about these plants. The aim of this review is to provide a comprehensive resource for anyone with an interest in divaricate plants.

First, we review past attempts at defining the divaricate habit and describing its variability in New Zealand. We propose a series of terms to try to standardise the vocabulary to be used when discussing these species (in bold in the text). We also report and discuss observations of divaricate-like species overseas, compiling a list of such occurrences.

We then review the published hypotheses that have been formulated to explain how such a diversity of architectures was selected in the New Zealand flora, and comment on the weight of evidence for or against each hypothesis. Finally, we examine the handful of studies that, rather than focusing on the evolution of these species, have looked at developmental aspects of these peculiar architectures. We conclude our review by pointing out new areas of research that might enhance our understanding of divaricate plants.

Characterising the diversity of divaricating habits: variations on a New Zealand theme

Past attempts at defining the divaricate habit in New Zealand

"Divaricate" comes from a Latin root meaning "stretched apart", which in botany refers to the usually wide angle at which branches of these species grow from the stem on which they originate. Indeed, the branching angle of divaricating species is on average more than 70°, sometimes over 90° (Bulmer 1958; Greenwood & Atkinson 1977), whereas their broadleaved relatives branch on average at < 55° (Kelly 1994). However, simplifying the definition of a divaricate species by its branching angle is misleading: Pott & McLoughlin (2014) and Pott et al. (2015) discussed the evolutionary adaptations of shrub or low-growing tree species of the extinct gymnosperm family Williamsoniaceae by making a parallel between them and New Zealand divaricates, claiming that they share similar architectures. Although the species they described undeniably branched at wide angles, they did not look anything like what New Zealand researchers call "divaricates": they bore much larger leaves (4-25 cm long, cf. < 2 cm in most New Zealand divaricates), and their branches were not interlaced. Likewise, many examples of extant species can be cited as having wide branching angles while not satisfying the definition of a divaricate, e.g. *Araucaria heterophylla* (Salisb.) Franco or *Piper excelsum* (G.Forst.). Indeed, the divaricate habit in New Zealand is also defined by a collection of other traits, including: small leaves (leptophyll and nanophyll classes of Raunkiær 1934); interlaced and abundant branching; relatively long internodes compared to the size of their leaves (Kelly 1994 and references therein; Maurin & Lusk 2020)—although some species show "short-shoot development" (Tomlinson 1978), i.e. stubby shoots with densely crowded nodes and leaves. The exact set of features used to define the habit however varies between authors (Kelly 1994; Grierson 2014; see Table

1 in Supplementary Material for a list of traits used by past authors). Finally, New Zealand divaricates are notably lacking in spines, except for *Discaria toumatou* Raoul which has spinescent congeners in Australia and South America. Some divaricating species, such as *Melicytus alpinus* (Kirk) Garn.-Jones and *Aristotelia fruticosa* Hook.f., have been considered spinescent by some authors (e.g. Greenwood & Atkinson 1977; Burns 2016), but we argue that their pointed branchlets are not sharp enough to pierce the skin and therefore probably did not have the same adaptive value as actual wounding spines or thorns.

Because the divaricate habit has evolved independently multiple times in the New Zealand flora, it appears under different structural forms that were tentatively grouped by various authors to form classifications. Bell (2008) recognised four branching pattern types in divaricate species: branching at wide angles (e.g. *Aristotelia fruticosa*), zig-zagging by sympodial (e.g. juvenile form of *Elaeocarpus hookerianus* Raoul) or monopodial (e.g. *Muehlenbeckia astonii* Petrie) growth, and "fastigiate". The use of "fastigiate" (meaning narrow branching angles) to categorise divaricate plants may seem paradoxical, but Bell's (2008) example, *Melicytus alpinus*, sometimes does show a fastigiate habit in shaded habitats. In our experience, however, in sunny environments *M. alpinus* has wider branching angles and is compactly interlaced. Tomlinson (1978) tried to assign divaricate species to Hallé et al.'s (1978) architectural models, without success. Halloy (1990) defined five groups based on branching patterns and assigned one species per group as examples, but his proposal has been largely ignored.

These variations around the features which characterise the divaricate habit led Wardle & McGlone (1988) to propose the word "filiramulate" to describe lianes and shrubs with reduced apical buds that have some (but not all) of the traits usually regarded as integral to the divaricate habit. These reduced buds exert a weakened apical dominance (Wardle & McGlone 1988), and

thus do not prevent the outgrowth of lateral branches. This first definition of the term "filiramulate" emphasised the wiry branches that may be flexuose to truly divaricating, and divaricate plants were therefore considered a type of filiramulate species. However, this definition of "filiramulate" has not been widely adopted by the scientific community.

The lack of a consensus word-based definition of the divaricate habit led to two attempts to find a mathematical quantification of divaricateness. Atkinson (1992) focused on branch density (number of lateral branches subtended per cm of main branch) and branching angle; Kelly (1994) also focused on branching angle, and included leaf size and density (the relative width of the leaves to the size of the internodes that bear them). Although these two indices emphasise different features of the divaricate habit, they correlate well for New Zealand species (Kelly 1994; Grierson 2014). In spite of these indices, which are rarely used in the literature, consensus definitions of the divaricate habit and its variations are still lacking.

Heteroblastic divaricate species

Although most of the species showing the divaricate habit keep it their whole life, some heteroblastic species produce a divaricating form early in life, then later switch to a non-divaricating form (Cockayne 1958). Very few quantitative data exist regarding the age before the non-divaricating form appears (Table 1), which may depend on the degree of exposure to sunlight in many cases (Cockayne 1958), or even on latitude at least in *Sophora microphylla* Aiton (Godley 1979). We propose referring to them as **heteroblastic divaricate** species; the term "habit-heteroblastic" used by Philipson (1963) for such species is inadequate as it does not mention "divaricate", and the juvenile and adults forms of some heteroblastic divaricate species do not only differ in architecture but also in leaf shape (e.g. *Pennantia corymbosa* J.R.Forst. & G.Forst.). Both forms often coexist on the same individual at least for some time, and the transition can be abrupt ("metamorphic" species (Ray 1990), such as in *Pennantia corymbosa*; see Figure 1 in

Table 1. Published quantitative measurements and estimations of the age reached by heteroblastic divaricate species before their adult form appears.

Species	Duration of the juvenile form	Reference
Elaeocarpus hookerianus Raoul	At least 60 years, depends on light conditions (source not specified by the author)	Cockayne (1958)
Prumnopitys taxifolia (D.Don) de Laub.	(1) Up to 60 years (source not specified by the author) (2) At least 47 years (based on ring counts)	(1) Dawson & Lucas (2012) (2) Lusk (1989)
Sophora microphylla Aiton	(1) ca. 15 years (source not specified by the author) (2) variable according to location: from absence of juvenile form in some parts of the North Island, to ca. 3.5 years in the Auckland region and at least 23 years in the south-east of the South Island (based on field observations and a common garden experiment)	(1) Cockayne (1958) (2) Godley (1979)

Supplementary Material), or gradual with transitional forms between the divaricating bottom and the non-divaricating top of the plant ("allomorphic" species (Ray 1990), such as in *Hoheria sexstylosa* Colenso). Day et al. (1997), studying the transition of the heteroblastic divaricate *Elaeocarpus hookerianus* from its juvenile form to its adult form, described a distinctive transitional form characterised by a less plastic growth pattern than the juvenile form, while not showing the morphological attributes that identify the adult form.

The ubiquitous use in the literature of the adjectives "juvenile" and "adult" (sometimes "mature") to name, respectively, the early divaricating form and the ultimate non-divaricating form of heteroblastic divaricate species, is potentially misleading. Jones (1999) criticised the use of "juvenile" to describe early forms of heteroblastic species because it better characterises a phase of plant development that is incapable of sexual reproduction. She therefore suggested that "juvenile" should be restricted to non-flowering stages of heteroblastic species. Yet, it was observed in New Zealand that the early form of some heteroblastic divaricate species are capable of flowering, such as those of *Pennantia corymbosa* (Beddie 1958; Cockayne 1958) or *Plagianthus regius* (Poit.) Hochr. subsp. *regius* (Cockayne 1958): they should therefore not be termed "juvenile". However, alternative terms such as "young" and "old" carry ambiguities of their own, so it is not obvious to us how to improve upon "juvenile" and "adult", which have become deeply anchored in the literature. We however recommend the use of **juvenile/ adult form** instead of the more commonly used juvenile/adult "stage" or "phase" to avoid the confusion between growth habit and reproductive state that Jones (1999) pointed out.

Two hypotheses have been proposed to try to explain the origin of heteroblastic divaricate species:

1. Hybridisation between a divaricate species and a non-divaricate relative

It is well known that some divaricate species hybridise with broadleaved congeners (e.g. Dansereau 1964; see lists of known (and

potential) hybrids compiled by Cockayne 1923, Cockayne & Allan 1934 and Greenwood & Atkinson 1977). These hybridisation events were hence proposed as a source for the origin of heteroblastic divaricate species (Godley 1979; 1985). Carrodus (2009) addressed the question of whether *Pittosporum turneri* Petrie, a heteroblastic divaricate small tree, is a hybrid between *Pittosporum divaricatum* Cockayne, a divaricating shrub, and *Pittosporum colensoi* Hook.f., a broadleaved tree. The study used plastid and nuclear DNA markers as well as a morphological analysis and found evidence supportive of such an event, e.g. that *P. tuneri* shows an ISSR band and morphological traits (for example in leaves, flowers and fruits) that combine those of the putative parents. They however suggested more investigation: their cross-pollination experiments between *P. divaricatum* and *P. colensoi* did not produce progeny, and given the limitations of the ISSR technique they recommend using more nuclear markers in more individuals. Shepherd et al. (2017) and Heenan et al. (2018) used chloroplast DNA and microsatellite markers respectively to study hybridisation and introgression events in New Zealand *Sophora* L.: even though their findings showed that these species hybridise readily, they reported little support for the hypothesis that the heteroblastic divaricate species *Sophora microphylla* arose through hybridisation between divaricate species *Sophora prostrata* Buchanan and the non-divaricate species *Sophora tetraptera* J.F.Mill.

However, as Godley (1985) makes explicit, his hypothesis allows for multiple generations after an initial hybridisation and for selection of the heteroblastic divaricate form from a variable population of hybrid derivatives (such as a hybrid swarm). Therefore, genetic signal of a hybrid origin might be weak and difficult to detect in studies employing only modest numbers of genetic markers.

2.   Neotenous loss of a putative adult non-divaricate form

A mirror image of the previous hypothesis, this hypothesis states that divaricate species arose from heteroblastic divaricate ancestors which later lost their forest-adapted adult form in response to new selective pressures in more open environments. It was first suggested by Cockayne (1911, p. 25–26; 1958, p. 141) and further developed by Day (1998a). It is difficult to see how to test such a hypothesis, which may explain why it has not been the subject of published research so far.

The divaricate habit in New Zealand and overseas

Variations of the divaricate habit are found in ca. 81 taxa in New Zealand (Appendix 1), including heteroblastic divaricate taxa. 80 are Eudicots, one is a Gymnosperm, and they represent 20 families. According to statistics about the New Zealand vascular flora produced by De Lange et al. (2006), this number represents almost 13% of indigenous woody spermatophytes. We refer to all these species as **divaricates**, a term that encompasses architectures that fall on a spectrum with two extremes. On one end, there are the **true divaricates** (or **truly divaricating** species), i.e. species with the most characteristic traits of the habit (such as tightly interlaced tough branches with relatively long internodes compared to leaf size, and leaves < 2 cm in length); typically shrubs that are common in open environments such as forest margins. To characterise the other end of the spectrum, we propose to use the term **semi-divaricate** as used by Greenwood & Atkinson (1977); these are species with traits that are not as typical as the traits of the true divaricates, such as slender branches in a more open architecture, and larger leaves—sometimes species that appear clearly divaricate in open areas tend towards a semi-divaricate habit when growing in the shade (Philipson 1963; Christian et al. 2006; pers. obs.).. Furthermore, we use the term **divaricate habit** to refer to the habit as a phenomenon, which manifests itself through a variety of architectures that we refer to as **divaricating habits**.

Although divaricates are present in a wide range of environments throughout New Zealand, several environmental patterns in their abundance have been noted. They

can be found in most forest types and successional shrublands (Wardle 1991), from the coast to alpine environments (Greenwood & Atkinson 1977). Divaricates have been reported as especially common in open environments such as forest margins (McGlone & Webb 1981), though relevant quantitative data are lacking. The percentage of divaricate species in woody assemblages increases from north to south (McGlone et al. 2010). Quantitative analyses have shown strong associations with frosty (and to some extent, droughty) climates such as are typical of the eastern South Island (Lusk et al. 2016; Garrity & Lusk 2017) where notably divaricate species often comprise the majority of arborescent assemblages (Lusk et al. 2016). It has been stated that divaricates are commonest on fertile young soils, such as those derived from recent alluviums or volcanic ashes (Greenwood & Atkinson 1977; McGlone et al. 2004). Consistent with this proposal, the largest known concentrations of divaricate species occur on alluvial terraces derived from mudstone in the Rangitikei and Gisborne areas (Clarkson & Clarkson 1994). However, an analysis of > 1,000 plots by Lusk et al. (2016) did not detect a significant association with terraces, or with any other topographic position.

Even though broadly similar plants occur in many other regions of the world, few of them show the full range of traits that are typical of New Zealand divaricates. Species showing aspects of the divaricate habit have been reported from Madagascar (Grubb 2003; Bond & Silander 2007), Patagonia (Wardle & McGlone 1988; McQueen 2000) or South America in general (Böcher 1977), mainland Australia and Tasmania (Bulmer 1958; Mitchell et al. 2009; Thompson 2010; Stajsic et al. 2015), Arizona and California in the USA (Carlquist 1974; Tucker 1974) and New Guinea (Lloyd 1985). The reported species and their close relatives indeed show branching patterns similar to what is seen in New Zealand divaricates, but they often present rather large leaves. This is for example the case with the North American *Quercus dunnii* Kellogg ex Curran,

reported by Tucker (1974), and the South African shrub species with dense, cage-like architectures studied by Charles-Dominique et al. (2017). Most overseas divaricate-like plants also differ notably from all but one New Zealand divaricates by the presence of wounding spines. A striking example is the African boxthorn (*Lycium ferocissimum* Miers; see Figure 2 in Supplementary Material), a South African species naturalised in New Zealand, which has tough interlaced branches similar to those of some New Zealand divaricates but bears sharp spines. However, this spinescence can sometimes be rather weak, for example in Australian species of *Melicytus* J.R.Forst. & G.Forst. (Stajsic et al. 2015). There are however some overseas divaricate look-alikes that show the same traits as New Zealand divaricates, for example *Tetracoccus hallii* Brandegee (Picrodendraceae), a non-spiny shrub with seemingly tough, interlaced branches, branching at wide angles and bearing small leaves (descriptions and pictures from SEINet Portal Network 2020 and Calflora 2020) from south-west USA (distribution data from GBIF 2020 and Calscape 2020).

We propose a list of the species that the studies cited above claim as "divaricate" and that we agree do resemble the architectural models we see in New Zealand divaricates (Appendix 2). We suggest the name **divaricate-like** to describe these species in order to emphasise their resemblance with New Zealand divaricates, yet stressing the fact that they often present distinguishing features (discussed above) and that they evolved in environmental conditions that were somewhat different from those experienced by the ancestors of New Zealand divaricates (reviewed below).

A review of theories about the evolution of New Zealand divaricates

The climatic hypothesis

Since its Upper Cretaceous separation from Gondwana (Wallis & Trewick 2009), New Zealand has undergone wide-ranging climatic changes. There is some debate as to the climate of the Upper Cretaceous: some argue this period was probably warmer than today (e.g. Fleming 1975), others that it was similar to present-day climates (e.g. Mildenhall 1980; Kennedy 2003). Hornibrook's (1992) review of marine fossil evidence indicates mostly subtropical climates during the Paleogene, although a sudden cooling event may have occurred around the Eocene-Oligocene boundary; temperatures then warmed to a local peak around 16 Mya, during the Miocene; the climate remained subtropical until a Late Miocene cooling, with further cooling from the Pliocene. The combined effects of this global cooling and of the rapid uplift of the Southern Alps during the Kaikoura Orogeny (Batt et al. 2000) created local frosty and droughty environments, especially in the eastern South Island. These new climates are likely to have reduced plant growth on many sites (Lusk et al. 2016), as shown by comparisons of juvenile annual height growth rates of the small broadleaved tree *Aristotelia serrata* J.R.Forst. & G.Forst. on modern sites that differ in growing season length (Bussell 1968; Anton et al. 2015).

Besides these climatic variations, a progressive submergence greatly reduced the extent of the New Zealand landmass from the Upper Cretaceous to the Early Miocene (85–22 Mya; Landis et al. 2008). It reaching a peak around 25–23 Mya known as the Oligocene marine transgression (Cooper 1989), at which point the surface of the New Zealand mainland was about 18% of its present-day surface area (Cooper & Cooper 1995). Landis et al. (2008) argued that, at that time, New Zealand was probably completely submerged, but this idea is now clearly refuted. Geological and paleobiological evidence show that New Zealand was not completely submerged during the Late Oligocene (reviewed by Mildenhall et al. 2014), particularly the 23 Myo Foulden Maar deposit (near Middlemarch, Otago), which notably contains fossils of diverse land plants (e.g. Lee et al. 2016). Moreover, recent molecular dating of the age of New Zealand lineages strongly suggest that some extant terrestrial plant and animal groups most probably originated from a Gondwanan vicariance (Wallis & Jorge 2018; Heenan & McGlone 2019).

Diels (1896) was the first to hypothesise an important role of Pleistocene climate in shaping the modern New Zealand flora, and as far as we are aware his work is the first attempt to explain the evolution of the divaricate habit. He proposed that, by reducing transpiration, the divaricate habit helped plants cope with droughty climates created in the eastern South Island by the uplift of the Southern Alps. Cockayne (1911) proposed that the divaricate habit was a response to past windy and droughty Pleistocene steppe climates, especially in the South Island. Similarly, Rattenbury (1962) hypothesised that the divaricate habit was an adaptation to dry or cool Pleistocene climates, and suggested an effect of the cage-like architecture as a windbreak, reducing transpiration. Wardle (1963) suggested that the divaricate habit continues to be adaptive in the present-day drier forest and shrub environments of eastern New Zealand.

McGlone & Webb (1981) further developed the climatic hypothesis, joining the debate started by Greenwood and Atkinson with the moa-browsing hypothesis (Greenwood & Atkinson 1977; see next section). They suggested that the divaricate habit represents the response of the "largely subtropical" Tertiary flora of the isolated New Zealand archipelago to the near-treeless glacial periods of the Pleistocene; this habit may have protected growing points and leaves from wind abrasion, desiccation and frost damage, which occurred unpredictably in the weakly seasonal New Zealand climates of the Quaternary. McGlone & Webb (1981)

also argued that the cage-like architecture of the divaricate habit also provides a milder microclimate within the plant which promotes higher rates of photosynthesis. The transition from the juvenile form to the adult form in heteroblastic divaricate species occurs above the height of the most damaging frosts during temperature inversions on clear nights, and the absence of the habit on offshore and outlying islands can be explained by their more oceanic, hence milder and less frosty, climates. Burns & Dawson (2009) however noted that the heteroblastic divaricate species *Plagianthus regius* from the mainland has a heteroblastic divaricate subspecies (*P. regius* subsp. *chathamicus* (Cockayne) de Lange) on the historically avian-browser-free Chatham Islands: they propose that, because *P. regius* is a recent immigrant on the Chatham Islands, its juvenile form has not been counter-selected yet.

The climatic factors suggested as selective forces are certainly not peculiar to New Zealand, whereas divaricate-like forms are much less common in other regions with similar climates (Dawson 1963). McGlone & Webb (1981) argued that what made New Zealand unique in the evolution of its subtropical flora in response to the cold, dry and windswept environments that appeared during the Quaternary was its isolation from sources of steppe-adapted floras, apparently believing that such floras might have provided plants with more conventional physio-morphological responses to cold, dry climates. This argument appears to overlook the fact that divaricate shrubs are also common in the Patagonian steppe, although those species are invariably spinescent (McQueen 2000). Furthermore, if wind was one of the drivers of the evolution of the divaricate habit, it is strange that few divaricate species are found in some very windy parts of New Zealand (Greenwood & Atkinson 1977): although they are often prominent in the vegetation of windswept areas such as Cook Strait (Wardle 1985), they present a low species richness there (Gillham 1960).

The photoprotection variant of the climatic hypothesis

Howell et al. (2002, see also Howell 1999), proposed that the shading of inner leaves by the cage-like divaricate architecture protects them from high irradiance on cold mornings after frosts, thus minimising photoinhibition and photodamage. It is a derivative of the climatic hypothesis that includes the effect of solar radiation as a selective pressure under stressfully cold climatic conditions. Howell et al. (2002) tested this hypothesis with an experiment involving the pruning of the outer branches of three divaricate species, which resulted in a reduced photosynthetic capacity of the inner leaves of these shrubs for at least 3 months. This experiment was criticised by Lusk (2002), who pointed out that the failure to include non-divaricate species as a control undermined the authors' conclusions: without further research, we cannot know if non-divaricate plants would respond in a similar way to pruning of their outer branches.

Empirical appraisal of the climatic hypothesis

Experimental tests have produced little support for the climatic hypothesis. Although past climatic conditions cannot be reliably reproduced in a controlled experiment, it is possible to estimate the differential response of divaricate and non-divaricate species when they are subjected to present-day climatic conditions similar to those hypothesised to have selected the divaricate habit during the Pleistocene.

Kelly & Ogle (1990) were the first to publish a test of the response of divaricating habits to climatic conditions. They studied the effect of air temperature, humidity, frost and wind on internal and external leaves of a divaricate species and both juvenile and adult forms of a heteroblastic divaricate species. While they did not show a significant difference in leaf temperature and air humidity between the inside and the outside of divaricating habits, they did show that the habit provides some protection against frost.

Keey & Lind (1997) used four species showing various divaricating habits to test the effect of different branching architectures on

the surrounding airflow patterns. Although they did not compare these species to non-divaricate species, they showed that dense branching patterns produce calmer zones, which may imply that they create a more favourable growing environment for leaves and other fragile organs by reducing wind damages.

Darrow and colleagues experimentally compared the frost resistance (2001) and water use efficiency (2002) of juvenile and adult forms of heteroblastic species, most of them divaricate at a juvenile stage. Darrow et al. (2002) found that most (though not all) divaricate juvenile forms had lower water use efficiency than the corresponding adult forms, concluding their results were not consistent with the climatic interpretation of the divaricate form. Darrow et al. (2001) compared the frost tolerance of the leaf tissues of juvenile and adult forms of five heteroblastic divaricate species by chilling leafy twigs overnight in thermostatically controlled freezers. However, their findings are of limited relevance to the climate hypothesis, as this approach does not address the effect of leaf size on night-time chilling under a clear sky (cf. Lusk et al. 2018), nor any potential effect of stem vascular anatomy on freeze-thaw embolism. In a similar vein, Bannister et al. (1995) studied the development of frost tolerance of detached leaves of some divaricate and non-divaricate species of *Pittosporum* Banks & Sol. ex Gaertn. over the course of autumn and winter. As was the case for Darrow et al. (2001) this study of tissue-level responses to frost did not test the potential roles of any of the characteristic leaf or stem traits of divaricates in conferring frost resistance .

A test of the photoprotection hypothesis was provided by Christian et al. (2006), who compared carbon gain versus structural costs of three congeneric pairs of divaricate and non-divaricate species under different intensities of light exposure. They showed that the costs of divaricating habits may be too high to be compensated by the photoprotection it provides, although they did not subject their samples to especially stressfully cold temperatures. In parallel, Schneiderheinze (2006) studied photoinhibition in divaricate and non-divaricate species under high light loads and other stressful conditions, such as drought. She found plants of both habits showed similar levels of photoinhibition under high irradiance, whether the plants were water-stressed or not. Here again, the hypothesis as formulated by Howell et al. (2002; i.e. protection from photoinhibition under cold conditions) was not tested, but the study still provided a valuable insight into the absence of significant photoprotection in divaricate species compared to their non-divaricate relatives.

Recently, an observational approach was taken by Lusk et al. (2016), who examined the environmental correlates of the proportion of divaricate species in arborescent assemblages throughout the main islands of New Zealand. They concluded that divaricate species are generally more diverse and prominent at frosty and droughty sites. Garrity & Lusk (2017) also used an observational approach by correlating climatic data with the distribution of 12 congeneric pairs of divaricate and larger-leaved species of the main islands of New Zealand. They found that divaricate species were significantly favoured by colder mean annual temperatures, and especially by colder minimum July temperature, but there was little evidence of an association with droughtier environments. Their results also showed little support for the photoprotection hypothesis, as divaricate species tended to predominate in cold environments irrespective of winter solar radiation levels. These two different observational approaches concur in showing that short frost-free periods and cold climates in general favour the abundance and diversity of divaricate species, but do not quite agree on the effect of drought. Given the limited number of species encompassed by Garrity & Lusk (2017), as well as evidence that the largest concentrations of divaricate species occur on middle North Island sites subject to significant water deficits (Clarkson & Clarkson 1994), the balance of the evidence

indicates that both frost and drought favour divaricate species.

Finally, a key component of the divaricate habit is small leaf size, which is known to be advantageous under harsh climates. A study by Lusk et al. (2018) compared leaf temperature during clear winter nights in relation to leaf size for 15 native New Zealand species, including four congeneric pairs of divaricate and non-divaricate species. They observed that small leaves chilled significantly less than large leaves. Their conclusions provide experimental support to leaf energy balance theory, which predicts that large leaves should be more vulnerable to frost because they cool below air temperatures on frosty nights whereas the smallest leaves stay close to air temperature (Parkhurst & Loucks 1972; Wright et al. 2017). Although this effect does not explain the three-dimensional structure of the divaricate habit, it suggests that the characteristically small leaves of divaricates may have provided an adaptive value in open habitats with short annual frost-free periods (see also Lusk & Clearwater 2015, a similar but less conclusive study on a smaller scale). Additionally, a study of the relationship between leaf dimensions and environmental variables in South African species of Proteaceae concluded that small leaves promotes convective heat dissipation under dry conditions and limited wind, enabling them to avoid overheating when water shortage forces stomatal closure (Yates et al. 2010). This effect was confirmed on Australian Proteaceae by Leigh et al. (2017). The small size of the leaves of most divaricates may therefore enable them to cope with drought better than large-leaved competitors.

The moa-browsing hypothesis

"Moa" is the Māori name for a group of now-extinct large (1-3 m and 10-250 kg; Atkinson & Greenwood 1989; Worthy & Holdaway 2002) flightless birds ("ratites") of the endemic order Dinornithiformes. Nine species are currently recognised, belonging to six genera and three families (Worthy & Scofield 2012). There are several hypotheses about how the ancestors of moa reached New Zealand (Allentoft & Rawlence 2012): they may have inhabited the New Zealand landmass from the time it started to separate from Gondwana about 80 Mya (the "Moa's Ark" of Brewster 1987); alternatively their ancestors might have reached New Zealand either by walking before 60 Mya, when the New Zealand landmass was still connected to a disintegrating Gondwana, or by flying after the complete separation. This last possibility is consistent with recent molecular evidence that the closest living relatives of moa appear to be tinamous (Phillips et al. 2010; Mitchell et al. 2014), a group of volant birds. If the earliest ancestors of moa to inhabit Zealandia were volant, fossil evidence suggest that their descendants have been large flightless birds since at least 16-19 My ago (Tennyson et al. 2010). All moa species were extinct by about the mid-15th century CE (Perry et al. 2014), apparently because of hunting (Allentoft et al. 2014).

Moa subfossil remains are more common on the South Island than on the North Island (Anderson 1989); moreover, they are more concentrated in the east of the South Island (Anderson 1989). However, this does not necessarily mean that moa were more abundant in the eastern South Island than elsewhere in the country, since the subfossil record is probably influenced by preservation biases: natural moa bone deposits are mainly in alkaline swamps and limestone caves, which are near-ideal preservation environments (Atkinson & Greenwood 1989) that happen to be more common in the eastern South Island than in most other parts of the country (Anderson 1989). Furthermore, an estimation of population size and distribution of the different moa species based on mitochondrial DNA and fossil record of *Dinornis* spp. suggests, in contrast, that moa populations were more numerous on the North Island than on the South Island (Gemmell et al. 2004). Therefore, it seems difficult at present to draw clear conclusions about geographic variation in moa densities.

Although the potential influence of moa browsing on the evolution of the divaricate

habit had been suggested by previous authors (e.g. Denny 1964; Carlquist 1974; Taylor 1975), Greenwood & Atkinson (1977) were the first to fully develop and argue this idea. First postulating that moa fed by clamping and pulling vegetation in the same manner as present-day ratites, they hypothesised that the tough and highly tensile branches of many divaricate species are difficult to tear off, while the interlaced structure kept leaves and growing tips out of easy reach. Hence, browsing on these plants would be less energetically rewarding than browsing on broadleaved species. Greenwood & Atkinson (1977) did not completely exclude a cutting ability of moa beaks, later acknowledging that the feeding behaviour of moa could not be confidently inferred because fossil skulls do not retain all the relevant tissues (Atkinson & Greenwood 1989). A recent study simulating the force of moa jaw muscles however concluded that different moa species fed in various different ways, including cutting (Attard et al. 2016). This appears to confirm the findings of studies of moa gizzard contents, which concluded that that divaricate twigs consumed by moa had been sheared rather than broken off (Burrows 1980; 1989; Burrows et al. 1981). These findings were later corroborated by a study of coprolites (Wood et al. 2008), yielding the same conclusion that divaricate species were by no means exempt from moa browsing (reviewed by Wood et al. 2020).

Moreover, Greenwood & Atkinson (1977) used evidence from the distribution of divaricate plants to support their hypothesis. One the one hand, they pointed out that divaricate plants often grow on lowland river terraces and swamps, which offer high nutrient levels and hence high plant productivity and nutrient content. They explained that divaricate species should be more subjected to moa browsing in such places, a sensible claim given that at least some studies show a positive correlation between herbivore abundance and soil fertility (e.g. Kanowski et al. 2001). Even if divaricate species have been reported from low fertility soils, such as the acidic soils of Stewart Island

(McGlone & Clarkson 1993), the largest known concentrations have been reported from fertile terraces derived from mudstone (Clarkson & Clarkson 1994). On the other hand, Greenwood & Atkinson (1977) noted that divaricates are largely absent from areas where moa did not live, such as offshore islands, or where moa could not reach them, such as growing on cliffs or as epiphytes. Although *Myrsine divaricata* A.Cunn. is abundant on some of the subantarctic islands of New Zealand (McGlone & Clarkson 1993; Meurk et al. 1994), which are unlikely to have harboured moa, Greenwood & Atkinson (1977) attributed such occurrences to recent colonisation from the mainland. Kavanagh (2015) lent support to this interpretation by comparing some traits used to describe the divaricate habit between related species of New Zealand mainland and Chatham Island (historically moa-free, with a flora largely derived from the mainland): he concluded that the absence of moa may have relaxed the selection for traits that deterred moa browsing on the main islands of New Zealand.

Greenwood & Atkinson (1977) also examined the bearing of the height of transition between the juvenile in adult forms in heteroblastic divaricate species on their hypothesis. They claimed that, in such species, the shift from the juvenile divaricate form to the adult non-divaricate form happens around 3-4 m high; this height corresponds to the approximate height of the tallest moa, implying that the adult form in these species only appears at heights where it is safe from browsing. Burns & Dawson (2006) brought support to this claim from New Caledonia: they mentioned that heteroblastic species there (which do not have a divaricating juvenile form) seem to shift form at about the estimated height of the flightless birds which once lived there, although they called for quantitative support for this observation. There are however multiple counter-examples to Greenwood & Atkinson's (1977) claim. Field observations sometimes reveal that the shift can happen significantly lower; for example, Cockayne (1911) reported that

the shift in *Sophora microphylla* can happen as low as 1.4 m, and we observed a shift in *Pennantia corymbosa* happening at about 2 m high (Figure 1 in Supplementary Material). Conversely, some homoblastic divaricate species can reach heights significantly above the size of the tallest moa without showing any relaxation of their divaricating habit; McGlone & Clarkson (1993) report such instances with individuals of *Coprosma crassifolia* Colenso, *Melicope simplex* A.Cunn. and *Myrsine divaricata* more than 5 m high; individuals of the latter species exceeding this height were also recorded by Veblen & Stewart (1980).

Finally, a crucial point of Greenwood & Atkinson's (1977) argument is the fact that the New Zealand flora is unique in having co-evolved with ratites but without browsing mammals. This phenomenon did not occur in areas where divaricate-like species co-evolved with ratites: in Madagascar, now-extinct elephant birds shared the island with giant tortoises and giant lemurs (Bond & Silander 2007); in Patagonia, Darwin's rhea grazed side-by-side with diverse mammals, such as equiids, camelids and giant ground sloths (McQueen 2000); in Australia, emus coexisted with many different herbivorous mammals, mostly marsupials (Roberts et al. 2001). Although these regions have all undergone megafaunal extinctions, they still host browsing mammals, and with the exception of Madagascar they have retained their ratites as well. No ratites or ratite fossils are known from North America; they are known only from former Gondwanan lands (Briggs 2003).

Greenwood & Atkinson (1977) originally hypothesised that the divaricate habit evolved as a deterrent to moa browsing. Lowry (1980) instead suggested that the main effect of the divaricate habit is to help the plant survive browsing by spacing and multiplying palatable growing tips, with a side-effect of making the browsing less energetically rewarding. This idea that the divaricate habit enables plants to survive rather than to prevent browsing led Atkinson and Greenwood to reconsider their 1977 hypothesis by acknowledging

Lowry's view (Atkinson & Greenwood 1980). Consequently, this view raised the question of why the divaricate habit, if it is not a specialised moa-deterring adaptation, is much scarcer in other regions where non-ratite browsers existed (McGlone & Webb 1981).

Indirect support for the moa-browsing hypothesis came from a fossil of a small-leaved woody species with wide-angle opposite branching that was discovered by Campbell et al. (2000). It was estimated to date from 20-16 Mya, which corresponds to the Early Miocene, whereas the climatic conditions usually put forward as the drivers of the evolution of the divaricate habit did not occur before the Pliocene (i.e. not before 5.333 Mya, Cohen et al. 2013, updated). Despite the absence of information about the three-dimensional structure of the plant when alive, 12 out of 15 experts they consulted agreed it was most likely a divaricate species (potentially extinct), and had rather varied ideas about what genus it could belong to. They noted the presence of "small acute broken processes protrud[ing] from the branchlets at irregular intervals", which look like spines even though they are not opposite. Even though the processes might have been defensive spines that would be of little use against moa beaks, this discovery appears consistent with the moa-browsing hypothesis.

According to the moa-browsing hypothesis, the divaricate habit could be nowadays seen as an anachronism (Greenwood & Atkinson 1977). As such, it was hypothesised that divaricate species may not be adapted to the current browsing pressure of introduced mammals because their costly ratite-resistant architecture was thought to be useless against mammals (Bond et al. 2004). Diamond (1990) imported the concept of "ghost" from overseas cases of anachronisms (later reviewed by Barlow 2000) when defending the hypothesis that divaricates are adapted to a now-extinct fauna. However, the conclusions of Pollock et al. (2007) about the preferences of ungulates for New Zealand woody plants, as well as a study by Lusk (2014) on the regeneration of divaricate and non-divaricate species in a forest remnant

that had been subject to ungulate browsing for decades, indicate that the divaricate habit may also be effective in deterring mammal browsing. Ungulates indeed tend to avoid some (though not all) divaricate species until more attractive foods are depleted (Forsyth et al. 2002; Lusk 2014).

Experimental appraisal of the moa-browsing hypothesis

The moa-browsing hypothesis was first tested experimentally by Bond et al. (2004), who fed juvenile and adult form foliage of two heteroblastic divaricate species to present-day ratites (emus and ostriches). They found that the high tensile strength of divaricate branches reduces breakage, that the high branching angles make the twigs difficult to swallow because birds cannot use their tongue to properly orient the twigs, and that small and widely spaced leaves increase the time and the energy required to consume leaf biomass. These results brought support to the hypothesis that the divaricate habit represents an adaptation to deter moa browsing. However, whether the feeding behaviour of the present-day ratites reliably reflect the feeding behaviour of extinct moa is a matter of debate (reviewed above).

A more elaborate cafeteria experiment was conducted a few years later by Pollock et al. (2007), comparing the offtake of deer, goats and ostriches from five divaricate species compared to five congeneric non-divaricate species. Their general finding is that features of the divaricate habit, such as small leaves and stem toughness, deter ungulates as well as ratites.

The moa-climate synthetic hypothesis

The idea that selection for the divaricate habit may have been driven by both past climatic conditions and the effect of moa browsing has been suggested several times since the debate started (Wardle 1985; 1991; Cooper et al. 1993; Bond & Silander 2007). Lusk et al. (2016) proposed a synthetic hypothesis with a specific mechanism integrating browsing and climatic factors. Although the ancestors of moa may have reached the New Zealand landmass as early as 80-60 Mya (reviewed by Allentoft & Rawlence 2012), the divaricate habit may not have become advantageous as an anti-browsing defence until Plio-Pleistocene climatic constraints on plant growth resulted in juvenile trees being exposed for longer to ground-dwelling browsers. During this period the combination of global cooling (Hornibrook 1992) and rapid uplift of the Southern Alps (Batt et al. 2000) created widespread frosty, droughty environments in the eastern South Island. The relatively fertile alluvial soils of these environments may have attracted high levels of browsing, but frost and drought would have reduced the ability of juvenile trees to grow rapidly out of the browsing zone, even in well-lit microenvironments such as treefall gaps. Evidence for a much earlier origin of divaricate plants, for example in the more benign climates of the Miocene or Oligocene, would refute both this hypothesis and the original climate hypothesis, and would point to moa browsing as the sole driver of divaricate evolution if no other factor can be identified.

The light trap hypothesis and its appraisal

The light trap hypothesis, formulated by Kelly (1994), relies on the conclusions of Horn (1971) that a multi-layered leaf distribution (i.e. leaves distantly scattered among multiple layers in the canopy) is more efficient at capturing a higher proportion of sunlight than mono-layered architectures (i.e. leaves distributed in a dense layer, the umbra of the outermost leaves completely obscuring the innermost leaves). Photosynthesis of most plants is indeed saturated well below full sunlight, the saturation point varying with, for example, species' successional status (e.g. Bazzaz & Pickett 1980). The scattered distribution of the leaves of divaricates over multiple branch layers therefore allows inner leaves to be in the penumbra of the outer leaves, thus better distributing light harvest throughout the canopy. The light trap hypothesis appears consistent with a modelling study of the impact of penumbral effects on shoot-level net carbon gain of

conifers (Stenberg 1995) which, like New Zealand divaricates, have small effective leaf diameters that result in short shadows; this modelling however does not explain the potential advantage of the architectural structure of divaricating habits. Moreover, even though penumbral effects are likely to result in higher carbon gain per unit area of foliage in small-leaved species growing in high light, Christian et al.'s (2006) data suggest that this advantage will be outweighed by the much higher (ca. threefold) leaf area ratio of congeneric broadleaved species, resulting in higher net carbon gain per unit of biomass in the latter. In divaricate species, this effect might be at least partially compensated by photosynthesis in stems, brought to light in one instance so far: the juvenile form of the heteroblastic divaricate *Prumnopitys taxifolia* (Banks & Sol. ex D. Don) de Laub. (Mitchell et al. 2019). More divaricate species will need to be investigated to determine how widespread stem photosynthesis is among divaricates. However, why would divaricating habits be scarce or absent in most other regions of the world if sunlight were the main driver of the evolution of these peculiar architectures in New Zealand, where solar irradiance levels are similar to those of other regions at comparable latitudes (Solargis 2020)? The light trap hypothesis does not appear to offer a satisfying explanation of the evolution of the New Zealand divaricates.

Insights into the development of divaricate branching patterns

If the debate surrounding divaricate plants has mainly focused on how the divaricate habit has evolved, a handful of studies looked into describing the range of growth patterns that give rise to the spectrum of divaricating habits, and how such patterns translate into adaptations to local environments.

Tomlinson (1978) examined bifurcation ratios of 18 New Zealand divaricates, including two heteroblastic divaricate species. He concluded that the interlaced structure of most divaricates is a consequence of a sequential branching which may be supplemented by reiterative branching.

Moreover, he suggested that this sequential branching is characterised by a lack of organisational control that translates into a dimorphism between orthotropic and plagiotropic branches. He recommended the study of the changes in the branching sequence of many divaricate species over their lifetime, as he believed this could be the only way to understand how the diversity of divaricating habits was produced under a possibly single selective pressure, and to draw general conclusions about their development.

Subsequently, the development patterns of a few divaricates were studied in the 1990s. The species were: *Muehlenbeckia astonii* (Lovell et al. 1991); the juvenile form of *Elaeocarpus hookerianus* (Day & Gould 1997; Day et al. 1998; Day 1998a), *Carpodetus serratus* J.R.Forst. & G.Forst. (Day 1998a; b) and *Pennantia corymbosa* (Day 1998c); *Sophora prostrata* and the juvenile form of *Sophora microphylla* (Carswell & Gould 1998). Overall, these studies concluded that such a growth pattern, with many growing points scattered across the plant's crown, offers a plastic structure that can more easily accommodate changes in environmental conditions (e.g. forest canopy gap versus closed canopy or seasonal changes in environmental conditions). These case studies also agreed that the lack of apical dominance plays a key role in the establishment of the divaricating habits they observed.

In parallel to the study of developmental patterns, a handful of studies looked into the hormonal control of the divaricate habit. Horrell et al. (1990) showed that a gibberellic acid treatment on cuttings of the adult form of *Pennantia corymbosa* and *Carpodetus serratus* tends to revert them to their juvenile form. This phenomenon did not occur in *Elaeocarpus hookerianus*, a result later confirmed by Day et al. (1998) with treatments of adult cuttings with gibberellic acid and other growth factors, including a cytokinin. Day et al. (1998) also showed that the adult form is not precociously triggered in *E. hookerianus* seedlings by these treatments. In *Sophora*, a treatment with 6-benzylaminopurine (a cytokinin) reinforces

the divaricateness of the juvenile form of *Sophora microphylla* (Carswell et al. 1996). Qualitative and quantitative measurements in *E. hookerianus* showed that the leaves of the divaricating juvenile form contain more active cytokinins than the non-divaricating adult form or transitional form leaves (Day et al. 1995, reviewed by Jameson & Clemens 2015). A similar yet more questionable conclusion was drawn from a comparison of the ratio of active to storage forms of cytokinin between divaricate and non-divaricate forms in *Sophora* species (Carswell et al. 1996). In contrast with the heteroblastic divaricate species studied, the levels of cytokinins are relatively low in the divaricate species *Sophora prostrata*, suggesting that they might not play a role in the establishment of the divaricating habit itself (Carswell et al. 1996). There are however too few studies about these growth regulators to formulate general conclusions about their potential effects in controlling the expression of the divaricate habit.

Conclusions

The terms **divaricate** or **divaricating** have been variously applied to around 80 New Zealand species that we regard as occupying a spectrum from **truly divaricate** (small and widely-spaced leaves; wide-angle branching; tough, wiry, tightly interlaced stems) to **semi-divaricate** (plants that present some but not all of these traits). This spectrum of architectural forms, which we call **divaricating habits**, is the expression of a phenomenon called the **divaricate habit**. **Heteroblastic divaricate** species have a divaricate (or semi-divaricate) **juvenile form** and a non-divaricate **adult form**, in contrast to the generally smaller (< 8 m) homoblastic divaricates that retain the divaricate form throughout their entire lives. Finally, we coin the term **divaricate-like** to describe overseas instances of the divaricate habit phenomenon, which acknowledges their resemblances with New Zealand divaricates while stressing their peculiarities. We hope that adoption of these terms will help reduce ambiguities in future research and facilitate clear communication. Our recommendations

nevertheless do not resolve the blurry boundary between true divaricates and semi-divaricates, like any categorisation involving a degree of subjectivity.

In spite of rather extensive experimental and observational evidence, no hypothesis about the evolution of divaricates in New Zealand has been decisively favoured over another. Among the most plausible hypotheses however, the moa-browsing hypothesis seems more supported than the climatic hypothesis, although neither are fully satisfying on their own. The synthetic moa-climate hypothesis has not been much discussed or tested so far, but given the evidence of both the moa-browsing hypothesis and the climate hypothesis individually, it appears to be a good candidate for a definitive answer to the divaricate question.

However, neo-ecological studies alone are unlikely to entirely resolve the origin of divaricate plants. One way still left to explore was suggested by Cooper et al. (1993): using molecular phylogenetics to date the divergences between divaricates and their closest non-divaricate relatives. Past studies estimating the age of New Zealand plant lineages (e.g. reviewed by Wallis & Jorge 2018; Heenan & McGlone 2019) have not focused on dating such divergences. Such studies, and studies on overseas groups that include New Zealand representative, can still offer isolated dates even though they might not have sampled the closest non-divaricate relative to the divaricate species they included (Appendix 3). The divergence dates between congeneric divaricate and non-divaricate species give us a first hint that the divaricate habit may have appeared less than 10 Mya in most cases. Table 2 provides the theoretical divergence dates one might expect from a study specifically dating splits between divaricate and non-divaricate species under the different hypotheses in play: the dates of the divergences in Appendix 3 hardly favour one hypothesis over the other, suggesting the need for a dating effort specifically targeting divaricate species and their closest non-divaricate relatives, as suggested by Cooper et al. (1993).

Table 2: Theoretical divergence periods between New Zealand divaricates and their closest non-divaricate relatives under the different hypotheses that try to explain their emergence. 5.3 Mya represents the lower bound of the Pliocene, the period when the climatic factors that would have favoured the evolution of the divaricate habit appeared.

Hypothesis	Implied theoretical divergence period
Climatic (including photoprotection)	Not older than ca. 5.3 Mya.
Moa-browsing	Much older than 5.3 Mya
Moa-climate synthesis	Not older than ca. 5.3 Mya.
Light trap	Unpredictable, as past sun radiation levels cannot be estimated (or with difficulty and questionable reliability).

There is still much to be done on developmental aspects of the divaricate form. First, our understanding of how the diversity of divaricating habits is produced needs more work despite having been the subject of numerous studies in the late 1990s. Second, the genes or gene networks that produce the diversity of divaricating forms have not been identified; such knowledge would help assessing Went's (1971) horizontal transfer hypothesis beyond theoretical arguments. These directions might even bring a new theory about the emergence of these species, or give birth to a new classification of the divaricating habits. However, we believe that such a new classification could only become consensual if it is based on quantitative measurements of the architectural features of all these species, that would be analysed by way of multivariate analyses. The main issue with such an endeavour is that each individual species will need to be measured in the wild, including several individuals in shaded and open habitats. Herbarium specimens cannot be used because the three-dimensional structure of the original individual is lost during pressing and, and only a small fraction of the architectural structure is usually represented. Such a classification may help significantly in clarifying the boundary between true divaricates and semi-divaricates, by identifying and discriminating architectural types within the spectrum of the divaricate habit. Moreover, combined with the molecular phylogeny suggested by Cooper et al. (1993), it will be essential to try to answer the following pending questions:

1. Did similar architectures arise in closely related species? I.e. do different divaricating habits reflect different inherited pre-existing traits of the corresponding lineages (as suggested for example in Brown & Lawton 1991)?

2. Did similar architectures arise in response to similar environmental selective pressures? I.e. what features of those architectures (e.g. branching angle, degree of interlacement, degree of branch toughness, etc.) were selected by climatic factors, moa browsing or another selective pressure yet to be identified? For example, do species typically found in open habitats present more interlaced and tougher branches than species of shaded environments, as field observations seem to suggest?

Finally, our understanding of the evolution of divaricate species in New Zealand might be aided by more extensive study of the ecology, morphology and evolutionary history of divaricate-like species in other regions of the world, which would lead to identifying the putative selective pressures under which they may have evolved. Generating a thorough inventory of divaricate-like species could be a useful first step that motivates further work on them.

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Supplementary Material

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Appendices

Appendix 1. Complete list of 81 New Zealand taxa falling on the divaricate habit spectrum. This list is based on a compilation of published work amended by field observations. Names of families follow the nomenclature of the APG (Stevens 2017). H = heteroblastic species showing the divaricate habit during early life stages only; D = strongly divaricate; ± = semi-divaricate.

Family	Taxon	Type of divaricate
Araliaceae	*Raukaua anomalus* (Hook.) A.D.Mitch., Frodin & Heads	D
Argophyllaceae	*Corokia cotoneaster* Raoul	D
Asteraceae	*Helichrysum lanceolatum* (Buchanan) Kirk	±
	Olearia bullata H.D.Wilson & Garn.-Jones	D
	Olearia hectorii Hook.f.	±
	Olearia laxiflora Kirk	D
	Olearia lineata (Kirk) Cockayne	±
	Olearia odorata Petrie	D
	Olearia polita H.D.Wilson & Garn.-Jones	D
	Olearia quinquevulnera Heenan	D
	Olearia solandri (Hook.f.) Hook.f.	±
	Olearia virgata (Hook.f.) Hook.f.	±
Elaeocarpaceae	*Aristotelia fruticosa* Hook.f.	D
	Elaeocarpus hookerianus Raoul	D, H
Fabaceae	*Sophora microphylla* Aiton	D, H
	Sophora prostrata Buchanan	D
Gesneriaceae	*Rhabdothamnus solandri* A.Cunn.	±
Lamiaceae	*Teucrium parvifolium* (Hook.f.) Kattari et Salmaki	±
Malvaceae	*Hoheria angustifolia* Raoul	D, H
	Hoheria sexstylosa Colenso	±, H
	Plagianthus divaricatus J.R.Forst. & G.Forst.	D
	Plagianthus regius (Poit.) Hochr. subsp. *regius*	D, H
Moraceae	*Streblus heterophyllus* (Blume) Corner	D, H
Myrtaceae	*Lophomyrtus obcordata* (Raoul) Burret	±
	Neomyrtus pedunculata (Hook.f.) Allan	±
Pennantiaceae	*Pennantia corymbosa* J.R.Forst. & G.Forst.	D, H
Pittosporaceae	*Pittosporum anomalum* Laing & Gourlay	D
	Pittosporum crassicaule Laing & Gourlay	D
	Pittosporum divaricatum Cockayne	D
	Pittosporum lineare Laing & Gourlay	D
	Pittosporum obcordatum Raoul	D
	Pittosporum rigidum Hook.f.	D
	Pittosporum turneri Petrie	D, H
Podocarpaceae	*Prumnopitys taxifolia* (Sol. ex D.Don) de Laub.	D, H
Polygonaceae	*Muehlenbeckia astonii* Petrie	D
	Muehlenbeckia axillaris (Hook.f.) Endl.	±
	Muehlenbeckia complexa (A.Cunn.) Meisn.	±
Primulaceae	*Myrsine divaricata* A.Cunn.	D
Rhamnaceae	*Discaria toumatou* Raoul	D

Appendix 1 (continued).

Family	Taxon	Type of divaricate
Rousseaceae	*Carpodetus serratus* J.R.Forst. & G.Forst.	D, H
Rubiaceae	*Coprosma acerosa* A.Cunn.	D
	Coprosma arborea Kirk	±, H
	Coprosma areolata Cheeseman	D
	Coprosma brunnea (Kirk) Cockayne ex Cheeseman	±
	Coprosma cheesemanii W.R.B.Oliv.	±
	Coprosma ciliata Hook.f.	D
	Coprosma crassifolia Colenso	D
	Coprosma cuneata Hook.f.	D
	Coprosma decurva Heads	D
	Coprosma depressa Colenso ex Hook.f.	D
	Coprosma distantia (de Lange & R.O.Gardner) de Lange	D
	Coprosma dumosa (Cheeseman) G.T.Jane	D
	Coprosma elatirioides de Lange & A.S.Markey	D
	Coprosma fowerakeri D.A.Norton & de Lange	±
	Coprosma intertexta G.Simpson	D
	Coprosma linariifolia Hook.f.	±
	Coprosma microcarpa Hook.f.	D
	Coprosma neglecta Cheeseman	±
	Coprosma obconica Kirk	D
	Coprosma parviflora Hook.f.	D
	Coprosma pedicellata Molloy, de Lange & B.D.Clarkson	D
	Coprosma polymorpha W.R.B.Oliv.	D
	Coprosma propinqua A.Cunn.	D
	Coprosma pseudociliata G.T.Jane	D
	Coprosma pseudocuneata W.R.B.Oliv. ex Garn.-Jones & Elder	±
	Coprosma rhamnoides A.Cunn.	D
	Coprosma rigida Cheeseman	D
	Coprosma rotundifolia A.Cunn.	D
	Coprosma rubra Petrie	D
	Coprosma rugosa Cheeseman	D
	Coprosma spathulata A.Cunn.	±
	Coprosma tenuicaulis Hook.f.	±
	Coprosma virescens Petrie	D
	Coprosma wallii Petrie in Cheeseman	D
Rutaceae	*Melicope simplex* A.Cunn.	D
Violaceae	*Melicytus alpinus* (Kirk) Garn.-Jones	D
	Melicytus crassifolius (Hook.f.) Garn.-Jones	D
	Melicytus drucei Molloy & B.D.Clarkson	D
	Melicytus flexuosus Molloy & A.P.Druce	D
	Melicytus micranthus (Hook.f.) Hook.f.	D
	Melicytus obovatus (Kirk) Garn.-Jones	±

Appendix 2. List of 53 divaricate-like taxa outside New Zealand, compiled from published work and personal observations. This list is non-exhaustive and is proposed as an initial step towards more thorough local inventories. Names of families follow the nomenclature of the APG (Stevens 2017).

Family	Taxon	Native distribution	Source
Anacardiaceae	*Schinus fasciculatus* (Griseb.) I.M.Johnst.	Patagonia	McQueen (2000)
	Schinus johnstonii F.A.Barkley	Patagonia	McQueen (2000)
Asteraceae	*Amphipappus fremontii* Torr. & A. Gray	South-western USA	Tucker (1974)
	Tetradymia axillaris A. Nels.	South-western USA	Tucker (1974)
Bignoniaceae	*Rhigozum madagascariense* Drake	Madagascar/Africa	Bond & Silander (2007)
Burseraceae	*Commiphora brevicalyx* H. Perrier	Madagascar/Africa	Bond & Silander (2007)
Cannabaceae	*Celtis pallida* Torr.	Southern USA	Tucker (1974)
Combretaceae	*Terminalia seyrigii* (H. Perrier) Capuron	Madagascar	Bond & Silander (2007)
Ebenaceae	*Diospyros humbertiana* H. Perrier	Madagascar/Africa	Bond & Silander (2007)
Fabaceae	*Adesmia campestris* (Rendle) Rowlee	Patagonia	McQueen (2000)
	Adesmia echinus C.Presl	Chile	Pers. obs.
	Chadsia grevei Drake	Madagascar	Bond & Silander (2007)
	Pickeringia montana Nutt.	California	Tucker (1974)
	Psorothamnus emoryi (A.Gray) Rydb.	Southern USA/ Northern Mexico	Tucker (1974)
	Psorothamnus polydenius (Torr.) Rydb.	South-western USA	Tucker (1974)
	Senna meridionalis (R. Vig.) Du Puy	Madagascar/Africa	Bond & Silander (2007)
Krameriaceae	*Krameria grayi* Rose & Painter	South-western USA	Tucker (1974)
Nyctaginaceae	*Bougainvillea spinosa* (Cav.) Heimerl	Patagonia	McQueen (2000)
Olacaceae	*Ximenia perrieri* Cavaco & Keraudren	Madagascar/Africa	Bond & Silander (2007)
Oleaceae	*Menodora spinescens* A.Gray	South-western USA	Tucker (1974)
	Olea oleaster Hoffmanns. & Link	Europe	Pers. obs.
Picrodendraceae	*Tetracoccus hallii* Brandegee	South-western USA/ Northern Mexico	Tucker (1974)
Pittosporaceae	*Pittosporum multiflorum* (A.Cunn. ex Loudon) L.Cayzer, Crisp & I.Telford	Australia	Relative to a pers. obs.
	Pittosporum spinescens (F.Muell.) L.Cayzer, Crisp & I.Telford	Australia	Pers. obs.
	Pittosporum viscidum L.Cayzer, Crisp & I.Telford	Australia	Relative to a pers. obs.

Appendix 2 (continued).

Family	Taxon	Native distribution	Source
Rhamnaceae	*Adolphia californica* S. Watson	California/Northern Mexico	Tucker (1974)
	Ceanothus ferrisiae McMinn	California	Tucker (1974)
	Ceanothus jepsonii Greene	California	Tucker (1974)
	Condalia globosa I.M.Johnst.	South-western USA/ Northern Mexico	Tucker (1974)
	Condalia microphylla Cav.	Patagonia	McQueen (2000)
Rosaceae	*Cercocarpus intricatus* S.Watson	South-western USA	Carlquist (1974)
	Coleogyne ramosissima Torr.	South-western USA	Tucker (1974)
	Cotoneaster atropurpureus Flinck & Hylmö	China	Relative to a pers. obs.
	Cotoneaster dammeri C.K.Schneid.	China	Relative to a pers. obs.
	Cotoneaster microphyllus Wall. ex Lindl.	Himalayas	Pers. obs.
	Cotoneaster perpusillus (C.K.Schneid.) Flinck & Hylmö	China	Pers. obs.
	Prunus fasciculata (Torr.) A.Gray	South-western USA	Tucker (1974)
	Prunus spinosa L.	Europe/Western Asia/North Africa	Pers. obs.
	Sarcopoterium spinosum (L.) Spach	Mediterranean Basin	Pers. obs.
Rubiaceae	*Coprosma nitida* Hook.f.	Australia/Tasmania	Thompson (2010)
	Coprosma quadrifida (Labill.) B.L.Rob.	Australia/Tasmania	Thompson (2010)
Salicaceae	*Azara microphylla* Hook.f.	Chile/Argentina	Pers. obs.
Solanaceae	*Lycium ameghinoi* Speg.	Patagonia	McQueen (2000)
	Lycium andersonii A. Gray	South-western USA/ Northern Mexico	Tucker (1974)
	Lycium brevipes Benth.	California/Northern Mexico	Tucker (1974)
	Lycium californicum Nutt. ex Gray	California/Northern Mexico	Tucker (1974)
	Lycium chilense Miers ex Bertero	Patagonia	McQueen (2000)
	Lycium ferocissimum Miers	South Africa	Pers. obs.
	Lycium fremontii A.Gray	South-western USA/ Northern Mexico	Tucker (1974)
	Lycium gilliesianum Miers	Patagonia	McQueen (2000)
	Lycium parishii A. Gray	South-western USA/ Northern Mexico	Tucker (1974)
Violaceae	*Melicytus angustifolius* (DC.) Garn.-Jones subsp. *divaricatus*	Australia	Stajsic et al. (2015)
	Melicytus dentatus (DC.) Molloy & Mabb.	Australia	Stajsic et al. (2015)

Appendix 3. Published divergence dates between New Zealand divaricate species and their closest sampled non-divaricate relatives. "+" = clade of species; "ca." = when no table with the date was available, it was estimated visually from the dated phylogeny; "or" = when different methods were used and gave different results.

Divaricate species	Sister non-divaricate species in the phylogeny	Estimated date of divergence (confidence interval if given)	Source
Aristotelia fruticosa Hook.f.	*Aristotelia serrata* (J.R.Forst. & G.Forst.) Oliv.	3 Mya (standard deviation: 0 My)	Crayn et al. (2006)
Coprosma, 31 taxa	*Coprosma,* 73 taxa (incuding the 2 Australian divaricate-like species listed in Table 1.2)	Between about 11 Mya (95% HPD: ca. 15-7 Mya) and 2.5 Mya (95% HPD: ca. 3-0.5 Mya)	Cantley et al. (2016)
Discaria toumatou Raoul	*Discaria chacaye* (G.Don) Tortosa	10.2 Mya (standard deviation: 3.7 My)	Wardle et al. (2001)
		3.94 Mya (95% HPD: 9.95-0.8 Mya)	Heenan & McGlone (2019)
Elaeocarpus hookerianus Raoul	*Elaeocarpus bancroftii* F.Muell. & F.M.Bailey + *Elaeocarpus arnhemicus* F.Muell.	4 Mya (standard deviation: 1 Mya)	Crayn et al. (2006)
Elaeocarpus hookerianus Raoul	*Elaeocarpus dentatus* (J.R.Forst. & G.Forst.) Vahl	13.13 Mya (95% HPD: 21.90-5.25 Mya)	Phoon (2015)
Lophomyrtus obcordata (Raoul) Burret + *Neomyrtus pedunculata* (Hook.f.) Allan	*Lophomyrtus bullata* Burret	ca. 4 Mya (95% HPD: ca. 9-1 Mya)	Thornhill et al. (2015)
Melicytus, 8 taxa	*Melicytus,* 15 taxa (including the 2 Australian divaricate-like species listed in Table 1.2)	From 6.41 Mya	Mitchell et al. (2009)
Muehlenbeckia (the 3 species listed in Table 1.2)	*Muehlenbeckia,* 16 taxa	From 20.5 Mya (95% HPD: 30.4-14.2 Mya), or from 22.3 Mya (95% HPD: 33.5-14.4 Mya)	Schuster et al. (2013)
Olearia solandri (Hook.f.) Hook.f.	*Olearia traversiorum* (F.Muell.) Hook.f.	ca. 1.8 Mya (95% HPD: ca. 3-1 Mya)	Wagstaff et al. (2011)
Pennantia corymbosa J.R.Forst. & G.Forst.	*Pennantia endlicheri* Reissek	0.9 Mya (95% HPD: 2.2-0.1 Mya)	Maurin (2020)
Plagianthus divaricatus J.R.Forst. & G.Forst.	*Plagianthus regius* (Poit.) Hochr.	3.9 Mya (95% HPD: 8.2-1.9 Mya), or 5.4 Mya (standard deviation: 2.2 My)	Wagstaff & Tate (2011)
Prumnopitys taxifolia (Sol. ex D.Don) de Laub.	*Prumnopitys andina* (Poepp. ex Endl.) de Laub.	ca. 14 Mya (95% HPD: ca. 29-7 Mya)	Leslie et al. (2012)
		11.75 Mya (95% HPD: 27.2-4.73 Mya)	Heenan & McGlone (2019)
Raukaua anomalus (Hook.) A.D.Mitch., Frodin & Heads	*Raukaua simplex* (G.Forst.) A.D.Mitch., Frodin & Heads	0.88097 Mya	Nicolas & Plunkett (2014)
		0.2 Mya (95% HPD: 0.6-0 Mya)	Maurin (2020)
Rhabdothamnus solandri A.Cunn.	*Coronanthera clarkeana* Schltr.	22.0 Mya (95% HPD: 29.5-18.0 Mya), or 17.9 Mya	Woo et al. (2011)
Rhabdothamnus solandri A.Cunn.	*Sinningia cooperi* (J. Paxton) Wiehler	26.44 Mya (95% HPD: 34.91-16.92 Mya)	Heenan & McGlone (2019)