


special issue: 

Feathers to Fur

The ecological transformation of Aotearoa/New Zealand

Comparative biogeography of New Zealand trees: species richness, height, leaf traits and range sizes

Matt S. McGlone^{1*}, Sarah J. Richardson¹ and Greg J. Jordan²

¹Landcare Research, PO Box 40, Lincoln 7640, New Zealand

²School of Life Sciences, University of Tasmania, Hobart, Australia

*Author for correspondence (Email: mcglonem@landcareresearch.co.nz)

Published on-line: 4 November 2009

Abstract: New Zealand forests grow under highly oceanic climates on an isolated southern archipelago. They experience a combination of historical and environmental factors matched nowhere else. This paper explores whether the New Zealand tree flora also differs systematically from those found in other temperate and island areas. A compilation of traits and distributions from standard floras is used to compare the New Zealand tree flora with those of Europe, North America, Chile, southern Australia, Fiji and Hawaii. New Zealand has a large number of trees (215 species ≥ 6 m in height). It is more tree-rich than temperate North America and Europe having up to 50% more species at a quadrat scale of 2.5° latitude x 2.5° longitude. However, this richness is due to a greater abundance of small trees (≤ 15 m in height) and we argue that it is a legacy of allopatric speciation and radiation during the late Neogene (2.5–10 million yrs ago) when the New Zealand landmass was repeatedly split into smaller island groups and mountain building occurred. The leaves of New Zealand trees, along with those of southeast Australia, are smaller and narrower than those of the temperate northern hemisphere. Dominance of the canopy by small-leaved evergreen conifers and angiosperms may have facilitated the persistence of small tree species in the lower canopy. The proportion of tree species with a deciduous or divaricating habit, and toothed-margin leaves, increases with latitude, suggesting a link with lower winter temperatures in the south. Tree species richness decreases with increasing latitude and, in conformity with Rapoport's Rule, latitudinal range width increases. Wide-range trees are mainly bird-dispersed, fast-growing seral small trees, or long-lived, tall podocarps. Wide-range trees appear to have no greater tolerance of climate extremes than narrow-range trees, and their persistence at high latitudes derives from their enhanced colonization ability.

Keywords: conifers; deciduous; divaricating; dispersal; diversity; leaf margin; leaf size; range size; Rapoport's Rule; tree height

Introduction

New Zealand's isolated position in the southern South Pacific, its highly endemic biota, oceanic climate and long separation from other continental landmasses makes it well suited to the generation and testing of biogeographic and ecological hypotheses. For example, New Zealand evidence has played an important role in understanding transoceanic dispersal (e.g. Crisp et al. 2009; Winkworth et al. 2005) and the impact of browsing birds (Lee et al. 2010), among other topics. However, comparative biogeographic analyses are few and this hampers attempts to make general statements about the New Zealand biota. In this review we look at New Zealand trees from a biogeographic perspective, with emphasis on some easily measured traits.

Trees are of disproportionate importance in biogeography. Firstly, they are of great functional importance as they provide most of the natural biomass and ground cover in boreal,

temperate and tropical regions, and can have extensive and cascading effects on other biota (Whitham et al. 2003). Secondly, their ecological importance, large size and (in temperate regions) moderate species richness, ensures that they are better documented than most other plant groups. And finally, while smaller plants often exploit restricted, specialist niches, the large size of trees connects them more closely to the prevailing macroclimatic and soil conditions and they are thus more easily related to the broader physical environment.

The distribution and ecology of New Zealand trees are reasonably well known. Most tree species of the New Zealand region have been described (Eagle 2006), comprehensive descriptions of New Zealand forests are available (Wardle 1984, 1991), and detailed reviews have been published for a number of dominant species. A comprehensive data base of forest plots has been established (National Vegetation Survey databank; Wiser et al. 2001). Advances have been made in modeling of tree distributions, abundance and relation to climate

variables (Leathwick 1995, 2001; Hall & McGlone 2006), and tree ecophysiology (e.g. Tissue et al. 2006). Nevertheless, relatively little is known about how functional traits influence the distribution of trees within the New Zealand archipelago, and systematic trait comparisons between New Zealand trees and those from other landmasses have not been made.

Here we use information available in standard floras and compilations to address these issues. Comparative data from other temperate regions and Pacific Islands are used to determine what is unique about the trees of the New Zealand archipelago, and to what extent they follow global patterns. We first present data on and discuss the species richness, distribution and morphological traits (height, leaf size and shape, deciduousness, divarication and frost resistance) of New Zealand trees in the context of other temperate areas. We then discuss some of the environmental and historical factors that have shaped these features of the tree flora, and why the New Zealand tree flora differs from floras of temperate areas elsewhere.

What is a tree?

Most publications fail to define what they intend by the terms *tree* and *shrub*. Even if they do so, many definitions are so vague as to be of only the broadest use: "Shrub: a woody plant of not very large size, and lacking a distinct trunk." (Allan 1961). Others are prescriptive and overly restrictive, excluding many species that might usefully be included: "A tree is a woody plant with an erect perennial trunk at least 7.5 cm in diameter at 1.3 m, a definitely formed crown of foliage, and a height of at least 4 m." (Little 1980); or so precisely inclusive that many species that most would regard as shrubs are included: "...any woody species reaching 3 m or more in any part of its range" (Adams & Woodward 1989). The lower height limit suggested as defining trees (or a forest canopy) varies from 2 m to 6 m. The contrasting problems of vagueness and excessive circumscription arise from the key features (woodiness, trunk number, stem diameters, height) being continuous variables. Even the apparently essential feature of the shrub – multiple stems – is not a discriminator. Some multi-stemmed woody species grow well in excess of 6 m high and are universally regarded as trees, and many small woody plants are monopodial. Moreover, the multi-stemmed shrub-like form can be environmentally induced.

Here, we will refer to self-supporting, woody species ≥ 6 m high as 'trees' and woody plants less than 6 m high as 'shrubs'. This makes structural sense because tall woody plants with obligate multiple stems (e.g. mallee eucalypts) usually have a maximum crown height of 5 m or less (Givnish 1984). A further advantage of using this definition is that compilations of 'trees' usually include almost all woody species ≥ 6 m but may use a variety of criteria with regard the inclusion of shorter species. In New Zealand, the 6 m minimum excludes nearly all woody plants confined to near tree-line situations in the so-called 'subalpine' scrub zone, thus giving a grouping largely restricted to forest. Analyses of tree distributions have often used a ≥ 3 m definition (Adams & Woodward 1989; Huntley 1993) and for comparative purposes, we have also developed a broader compilation that includes such species. To avoid confusion, here we refer to this broader grouping of all woody plants ≥ 3 m as 'arborescents'. We refer to trees ≤ 15 m as 'small trees' and those > 15 m as 'canopy trees'.

Data sources and analysis

For New Zealand, we used the Landcare Research Ngā Tipu Aotearoa – New Zealand Plants website to validate taxon names and check distributions. For height, fruit type, leaf and range measurements, we used Allan (1961), supplemented by data from Eagle (2006), Salmon (1980) and Wilson (1993). We used measured seed masses of 162 arborescents (Peter Bellingham, Sarah Richardson, Susan Wiser unpub. data) and arborescent seed lengths as given in Webb & Simpson 2001. We used standard comprehensive temperate floras which systematically recorded tree height and leaf dimensions, from North America north of Mexico (Elias 1980), northwest America (Hitchcock et al. 1964), Europe (Tutin et al. 1964), Chile (Rodríguez et al. 1983) and southeastern Australia (Curtis and Morris 1963; Foreman & Walsh 1993) to obtain a representative sample of self-supporting woody plants. In some analyses of the North American data we split the data set into eastern and western provinces following definitions given in Elias (1980) or analysed northwestern North America or the state of Florida separately. Our definition of tree (≥ 6 m) mostly excludes specialist woody plants of arid or cold environments. Given New Zealand's position in the Pacific and its strong biogeographic connections with the islands to its north, we have included Hawaii (Wagner et al. 1990) and Fiji (Smith 1979).

For all measurements we have taken the upper figure of a given normal range, excluding formulations such as "occasionally reaching...". Where sources disagreed as to height, we generally accepted the tallest measurement on the basis that there is a tendency for somewhat low average heights to be reported.

Heights and leaf dimensions of woody plants reported in floras are approximations, characterized by rounding up to whole numbers, estimates to the nearest multiple of 10 and a strong aversion to odd numbers. These trends have been used to guide assignment of flora tree heights and leaf sizes to 'bins' for analysis. Given the large number of species involved in this survey, and the limited descriptors available, no attempt was made to account for different shapes of leaves when calculating areas; the formula used to approximate this value was $length \times breadth \times 2/3$ (Cooper 1960). Compound leaves were represented by the largest leaflet, which was treated as a single leaf in our analysis. Where a single leaf was cut nearly through to the mid-rib by deep sinuses such as to make the leaf a functional compound leaf, the pseudoleaflets were used in the analysis.

In the leaf analyses we exclude ferns, conifers, monocots and palms because the unusual dimensions of leaves of these types relative to most dicots, combined with their variable representation in the different floras, distorts the analyses. All correlation analyses use Pearson's coefficient.

Numbers, distribution and traits of the arborescent flora

How many tree species are there in New Zealand?

We recognize 614 self-supporting woody plant species in the New Zealand archipelago (Kermadecs to Campbell Island), of which 26 are confined to offshore islands (those not connected to the three mainland islands during low glacial sea levels). There are 321 arborescents (i.e. ≥ 3 m tall), of which 215 are trees (i.e. ≥ 6 m tall) and 44 of these are canopy trees (> 15 m). Trees include 17 conifers, 6 tree ferns and 2 palms.

Table 1. Features of the tree floras in seven regions. Species richness is given as number of species, and in parentheses trees as a percentage of the vascular flora. Trees are defined as ≥ 6 m. For flora sources see text.

Territory	Vascular spp.	Tree spp. (≥ 6 m)	Tall trees spp. (>15 m)	Gymnosperm spp. (≥ 6 m)	Median tree height (m)	Land area (10^4 km 2)
New Zealand	2220	215 (9.7%)	44 (2.0%)	17	10	27
North America†	15352	582 (3.8%)	295 (1.9%)	93	12	2025
Europe	10500	186 (1.8%)	85 (0.8%)	31	15	1004
Victoria (Australia)	4612	232 (5.0%)	81 (1.8%)	5	12	28
Tasmania (Australia)	1700	141 (8.3%)	34 (2.0%)	6	14	6
Hawaii	956	199 (20.8%)	16 (1.7%)	0	8	3
Fiji	1318	522 (39.6%)	184 (14%)	9	14.5	2

† north of Mexico

Is New Zealand tree rich?

Trees form a larger proportion of the New Zealand vascular flora than in other temperate regions (Table 1). However, the New Zealand flora has relatively few herbaceous plants when compared with other temperate floras, so this is a misleading statistic. When absolute numbers are compared, New Zealand has more tree species than the whole of Europe in less than 3% of the land area and 37% of the tree species richness of North America (north of Mexico) in 1.1% of the land area, and about the same number as Victoria in roughly the same area (Table 1). However, as these regions vary considerably in climate, area is also a misleading basis for comparison. A more relevant assessment of richness can be obtained through holding area constant and controlling for climatic factors or plant productivity, both often suggested as being related to species richness (Field et al. 2005; O'Brien 2006).

Adams & Woodward (1989) demonstrated for temperate regions a close positive relationship between global arborescent richness in 2.5° longitude \times 2.5° latitude quadrats and net primary production. They included 4 New Zealand quadrats, which fell on the upper edge of the global envelope of richness versus productivity. Our compilation suggests that they underestimated the number of species in New Zealand. The statistical relationship between arborescent richness and

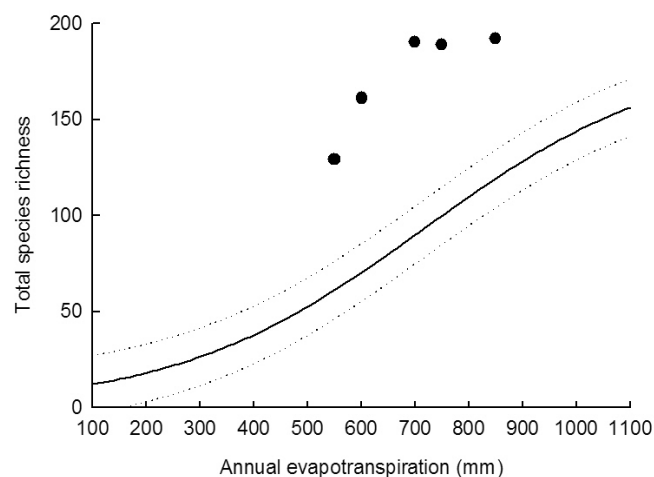


Figure 1. New Zealand arborescent richness (circles) in $2.5^\circ \times 2.5^\circ$ latitude/longitude quadrats versus observed values for sea level evapotranspiration. Solid curve: arborescent species richness from the evapotranspiration-richness equation developed in Currie & Paquin (1987); dotted curves ± 15 species.

evapotranspiration developed by Currie & Paquin (1987) for USA and Canada indicates that New Zealand has 60–130% more trees than the global trend (Fig. 1). Only the most tree-rich quadrat of the United States (southeast with 180 species; Currie & Paquin 1987) exceeds the New Zealand average. For a temperate region, New Zealand is rich in tree species.

Adams & Woodward (1989) noted that, even though New Zealand is isolated and has an almost entirely endemic aborescent flora, it has about the same number of species as areas with similar climates. In their view, this made an independent equilibrium of tree species with climate a much more likely scenario than one relying on geographical or historical factors. However, empirical equations such as these may only be valid for the regions for which they were developed and, as shown above, global equations are poor at estimating New Zealand's aborescent richness.

Although New Zealand's tree richness is strongly correlated with climate at a regional scale (Leathwick 2001), we doubt that current energy–water measures provide a mechanistic explanation for arborescent species richness at smaller or larger scales. Bellingham et al. (1999) analysed tree (defined as individuals with trunks at 1.4 m height >10 cm diameter) richness on a 400 m 2 plot scale throughout New Zealand (a total of 687 plots in 14 catchments spanning 37° to 46° S), and showed that tree richness and diversity declined with increasing altitude and latitude, both surrogates for available energy. However, when the average tree richness in these plots in separate regions is compared with canopy tree (>15 m) richness as recorded by latitudinal band in this present study, there is no strong correlation ($r = 0.24$; $N = 14$). In other words, regional richness does not contribute to local richness at a 400 m 2 scale. Presence of *Nothofagus* greatly reduces tree richness even when sites are controlled for environmental factors (Leathwick & Austin 2001) but the correlation between regional (this study) and local (Bellingham et al. 1999) richness is not markedly improved when beech-dominant sites are removed ($r = 0.25$; $N = 11$).

The three scales for tree richness (plot, regional and global) are thus decoupled. That is, although tree richness within New Zealand can be predicted by latitude, and by environmental factors over a regional scale, there is little or no relationship between this regional scale and the typical plot scale, nor can tree richness be estimated by global equations empirically derived from other temperate landmasses. We propose that evolutionary and geological history determine the numbers of trees at the archipelago scale, past climatic fluctuations sort them across landscapes, and current environments control local richness (McGlone 1996; Ricklefs 2006). What then are these

historical factors that explain the comparative abundance of trees in New Zealand? We will deal with this question after a consideration of tree height and leaf size.

Height of New Zealand trees

Actual tree heights are determined by phenotypic plasticity in response to environment, and genotypic limitations to maximum height. The maximum height for any tree has been estimated at 122–130 m due to water stress imposed by increasing gravity and path length resistance (Koch et al. 2004), but few trees reach even half this maximum. Regardless of genetic limitations, trees grow tall under conditions where growth is optimized, i.e. where soils are nutrient rich, the climate moist year-round, and stresses such as drought, high vapour pressure deficit and chronic wind are minimal, and where disturbance is infrequent enough that slow-growing trees can reach their maximum (King 1990). Conversely, tree species attain lower heights under dry climates, on soils characterised by low nutrients and poor drainage, and where exposed to chronic wind stress.

New Zealand mainland tree species have a median height of 10 m (somewhat less for offshore island endemics at 9 m); median heights for trees in other temperate areas vary between 12 and 15 m (Table 1). The trees of tropical Fiji are similar in size to those of the temperate region (median 14.5 m). On the other hand, North American trees confined to subtropical Florida (median 10 m), and those of Hawaii (median 8 m) are as small or smaller than those in New Zealand.

All the woody floras examined here show a similar strongly right-skewed height distribution approximating a reverse-J curve, and therefore fitting the general pattern for most classes of organisms (Fig. 2; Aarssen et al. 2006). However, we included widely disparate floras, with some from almost completely forested regions (Fiji) and others from regions with considerable areas of grassland, steppe or desert (Europe, North America). New Zealand, being largely forested, has a relatively high proportion of trees compared with temperate continental regions, but with a marked excess of small trees, and few ≥ 30 m (Fig. 2). The floras studied here form three groups based on the relative proportions of height categories (Figs 3 & 4):

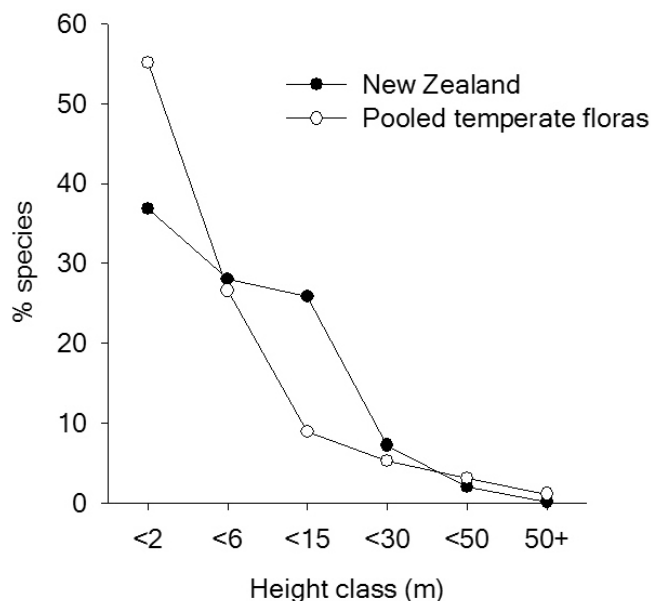


Figure 2. Height distributions for all woody species in New Zealand and for a pooled temperate woody flora (Europe west of the Urals, northwestern North America, Tasmania and Victoria).

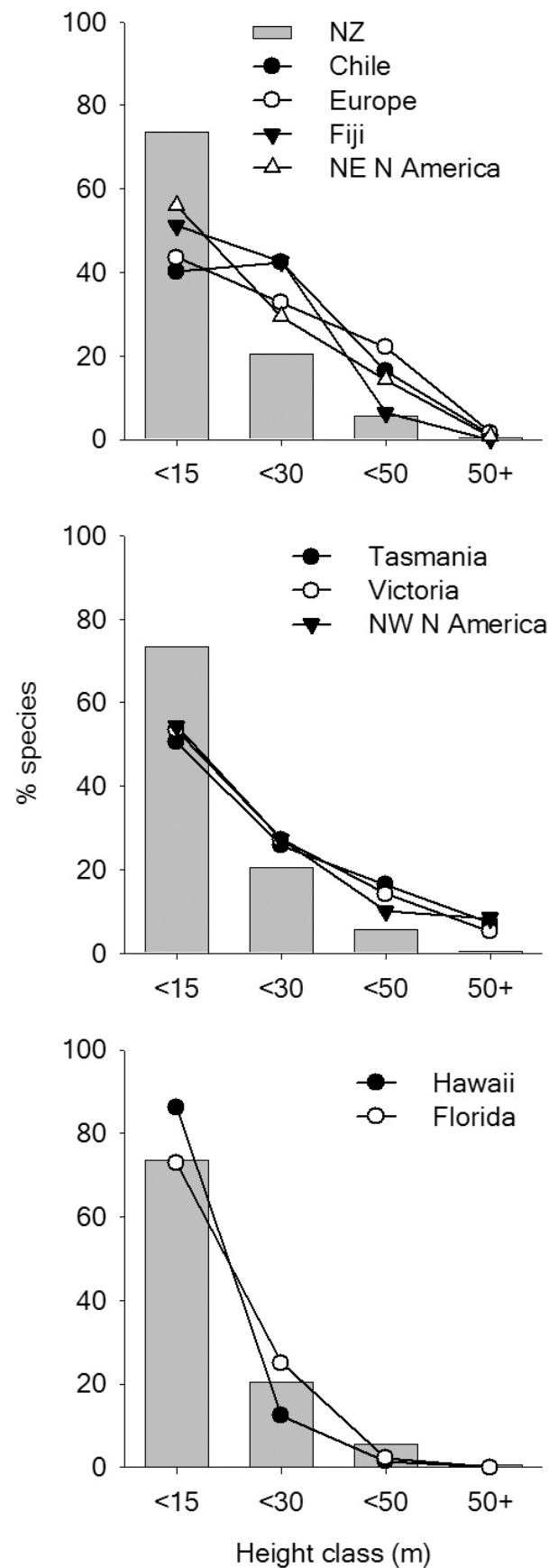


Figure 3. Height distribution for trees (≥ 6 m) in New Zealand (bars) compared with (lines): (a) Chile, Europe (west of the Urals), eastern North America (east of approximately 103°W), and Fiji; (b) Tasmania and Victoria (both Australia), western North America (west of approximately 103°W); (c) Hawaii, and Florida (trees not shared with rest of eastern North America).

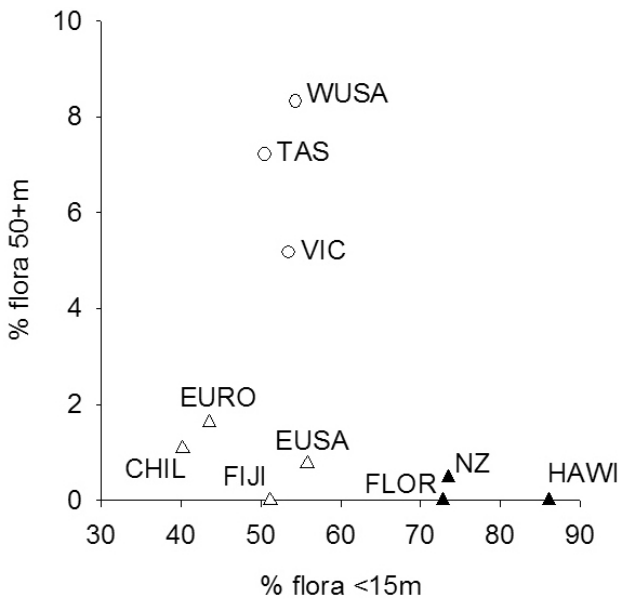


Figure 4. Percentage of trees ≥ 50 m versus percentage of trees < 15 m for all floras. WUSA = Western North America; TAS = Tasmania; VIC = Victoria; EURO = Europe west of the Urals; CHIL = Chile; EUSA = Eastern North America; FIJI = Fiji; NZ = New Zealand; FLOR = Florida; HAWI = Hawaii. Symbols correspond to the three groups discussed in text.

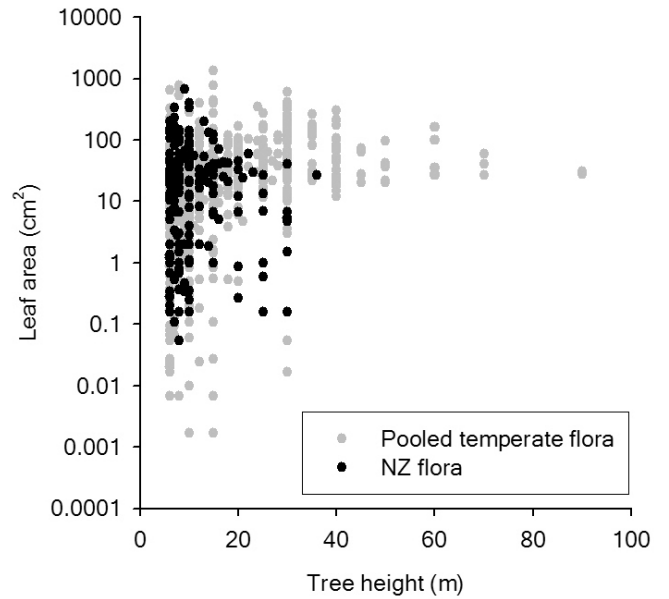


Figure 5. Leaf area versus tree height for temperate floras from Europe, Western USA, Tasmania and Victoria (pooled, in grey) and New Zealand (black).

- (1) Europe, eastern North America, Fiji and Chile, which have a high proportion of trees > 15 m and < 50 m,
- (2) western North America, Victoria and Tasmania, which are characterised by a high proportion of trees ≥ 50 m,
- (3) New Zealand, Hawaii and Florida, which have high proportions of tree species ≤ 15 m, a relatively low percentage > 15 m and < 50 m, and few or none ≥ 50 m.

Compared with those of other temperate regions, New Zealand trees are clearly shorter on average and its tallest trees shorter than tallest trees elsewhere.

Leaf size of New Zealand trees

Width is perhaps the most influential leaf dimension in that it dominates light interception and energy exchange. Wider

leaves cast longer, darker shadows (Horn 1971) and have thicker boundary layers, which slow energy and gas exchange (Parkhurst & Loucks 1972; Schuepp 1993). Large leaves thus warm more, are more drought sensitive and more vulnerable to chilling (Lambers et al. 2008). Broad, densely-shading leaves held in a relatively shallow canopy can be thought of as a strategy which may not maximise energy capture (that is done by a deep, multi-layered canopy), but can prevent the invasion of competitors, including lianas, (Falster & Westoby 2003). Leaf area tends to be much larger under warm, moist climates (Webb 1968) than under cool dry climates (Givnish 1984), although there is a great range under any particular climatic regime.

Mean leaf area of New Zealand dicotyledonous trees does not differ markedly from that of the pooled temperate floras,

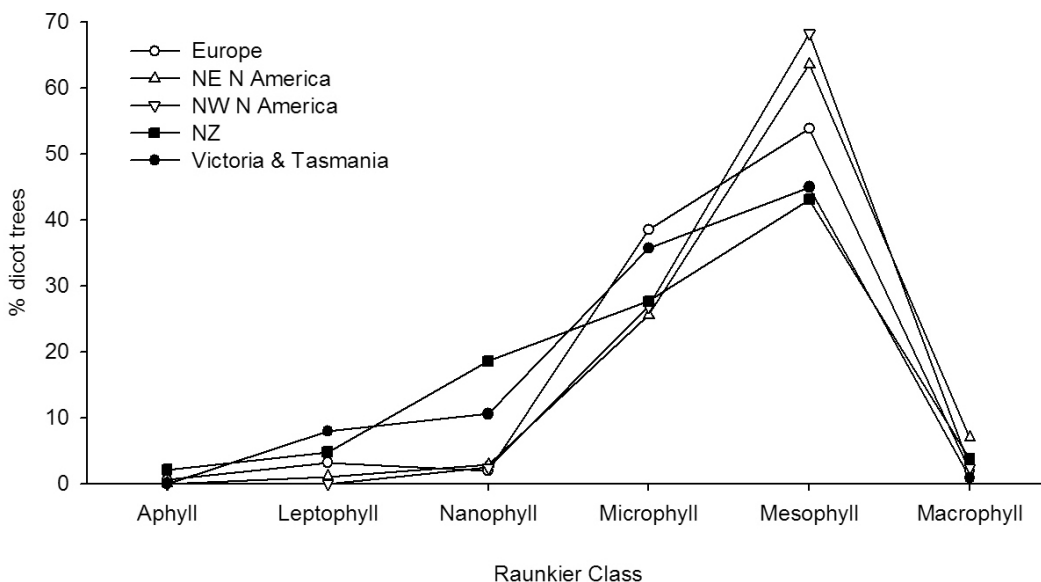


Figure 6. Raunkier leaf size spectra for dicotyledonous trees in five temperate floras. Note: NE North America excludes Florida because of its subtropical nature; and northwestern North America, is from northernmost California northwards. Leaf area calculated using $0.66 * \text{leaf length} * \text{leaf width}$ (Cooper 1960).

except that the mean leaf areas of species ≥ 20 m or more in height (tall canopy trees) are almost an order of magnitude smaller than those of the pooled temperate floras (Fig. 5). Standard Raunkier size classes show that the temperate floras form 2 distinctive groups (Fig. 6). All floras have a maximum percentage in the mesophyll class, but in Europe, northeastern and northwestern North America, mesophylls make up $>50\%$ of the total, while nanophylls and leptophylls are uncommon. New Zealand, Tasmania and Victoria have $<45\%$ mesophylls, but nanophylls and leptophylls are relatively abundant. New Zealand trees, by this measure, do not differ significantly from the other evergreen southern floras but favour smaller leaf classes than northern hemisphere floras.

New Zealand trees have mean leaf widths greater than those of Tasmania, Victoria and Chile, are approximately the same as those of western North America, but are substantially narrower than those of Europe, eastern North America and northwestern North America (Table 2). If evergreen-only leaf widths are compared, New Zealand leaves are closer to but still narrower than those of Europe and eastern USA, but wider than those of northwestern and western North America. Thus, the width of New Zealand evergreen tree leaves is close to those of evergreen trees from the Northern Hemisphere. The much narrower evergreen leaves of the Tasmanian and Victorian trees probably results from the lower rainfall and poorer soils of those states (McDonald et al. 2003).

New Zealand trees that occur at low latitudes have leaves 40% wider and more than twice the area of those that occur at high latitudes (Table 3). The taller (>15 m; $N = 28$) dicotyledonous trees in New Zealand have leaves about one third less in width than those of the smallest (6–10 m; $N = 129$) trees ($29.2 \text{ mm} \pm 3.4$ versus $39.3 \text{ mm} \pm 3.7$) and, in this, differ from all the other floras except Hawaii. We surmise

that leaves of temperate evergreen dicotyledonous trees that grow at high latitudes or are exposed in the canopy are more affected by cold, wind, low atmospheric moisture and drought than subcanopy species or deciduous species, and are therefore smaller.

Latitude, mean annual temperate and species richness in New Zealand arborescents

Arborescent species richness shows distinctly different latitudinal trends for different size classes (Fig. 7a). Species richness is greatest at 37–39°S in all but the smallest size class (tall shrubs, 3–5 m). From 38°S, canopy tree richness (>15 m) falls steadily southwards, but small trees (6–15 m) have approximately constant species richness until 42°S then decline. In contrast, the richness in the smallest size class (3–5 m) peaks at 42°S. The lower species richness in latitudes north of 37°S in New Zealand is likely to be due to the small land areas in these latitudes.

Arborescent richness per 1° latitudinal band has a moderate positive correlation ($r = 0.70$) with mean annual temperature at sea level in the west (i.e. areas not limited by water availability). If the Northland Peninsula is excluded, the correlation coefficient strengthens to 0.98.

Latitude, divarication, deciduousness and leaf margins in New Zealand arborescents

Divarication, deciduousness and leaf margin type (entire versus toothed) have all been suggested as traits related to New Zealand climate (McGlone et al. 2004; Kennedy et al. 2002). Divaricating and deciduous arborescent species rise as absolute numbers and proportions with increasing latitude (Fig 7b) and therefore have strong negative correlations with sea level mean

Table 2. Leaf widths (mean in mm \pm SE, and median in parentheses) for trees of selected temperate floras (excluding conifers, ferns, and monocots). Florida includes only trees found there and not elsewhere in North America. Floras are arranged in ascending order of mean leaf width for all species.

Flora	All species	Deciduous†	Evergreen
Tasmania	21.5 \pm 1.7 (22)	na	21 \pm 1.7 (22)
Victoria	25.6 \pm 1.7 (20)	na	25.6 \pm 1.7 (20)
Chile	30.6 \pm 2.2 (25)	30.4 \pm 6.8 (30)	30.7 \pm 2.2 (25)
New Zealand	38.0 \pm 2.7 (30)	30.7 \pm 8.2 (15)	38.6 \pm 2.8 (30)
Western USA	43.4 \pm 3.3 (35)	47.5 \pm 4.7 (38)	35.7 \pm 2.9 (30)
Florida	43.8 \pm 3.4 (40)	34.4 \pm 8.3 (40)	44.9 \pm 3.6 (40)
Europe	46.7 \pm 2.4 (40)	47.8 \pm 2.6 (40)	43.4 \pm 6.7 (40)
Northwestern North America	58.7 \pm 7.6 (50)	62.6 \pm 8.6 (50)	35.8 \pm 8.5 (35)
Eastern North America	61.4 \pm 2.7 (50)	64.8 \pm 3.0 (50)	42.7 \pm 3.9 (39)

†Victoria has no deciduous species, Tasmania has only one, and all other floras have ≥ 10 deciduous species.

Table 3. Summary of New Zealand tree characteristics according to range size. Data are presented for the whole tree flora, for species with narrow range sizes (1°–3°) versus wide range sizes (11°–13°), and those that occur at low latitudes (35°S–37°S) versus high latitudes (45°S–47°S). Ferns, conifers, monocots and offshore endemics were excluded from the analysis.

Tree range or latitude	N spp	Height (m)	Leaf width (mm)	Leaf area (cm ²)	Proportion entire leaved	Mid range point (°S)	Proportion bird-dispersed
All species	173	11.2 \pm 0.56	36.8 \pm 2.7	39.2 \pm 5.6	0.67	39.4 \pm 0.2	0.51
narrow 1–3°	46	8.8 \pm 0.6	37.0 \pm 6.3	50.1 \pm 16.1	0.80	38.4 \pm 0.5	0.38
wide 11°–13°	44	11.8 \pm 1.0	33.1 \pm 4.2	26.3 \pm 5.3	0.57	40.6 \pm 0.1	0.77
low 35°–37°	168	11.7 \pm 0.6	42.5 \pm 3.5	47.5 \pm 7.6	0.68	38.4 \pm 0.2	0.61
high 45°–47°	76	11.3 \pm 0.8	30.5 \pm 3.1	23.3 \pm 3.6	0.55	41.5 \pm 0.2	0.57

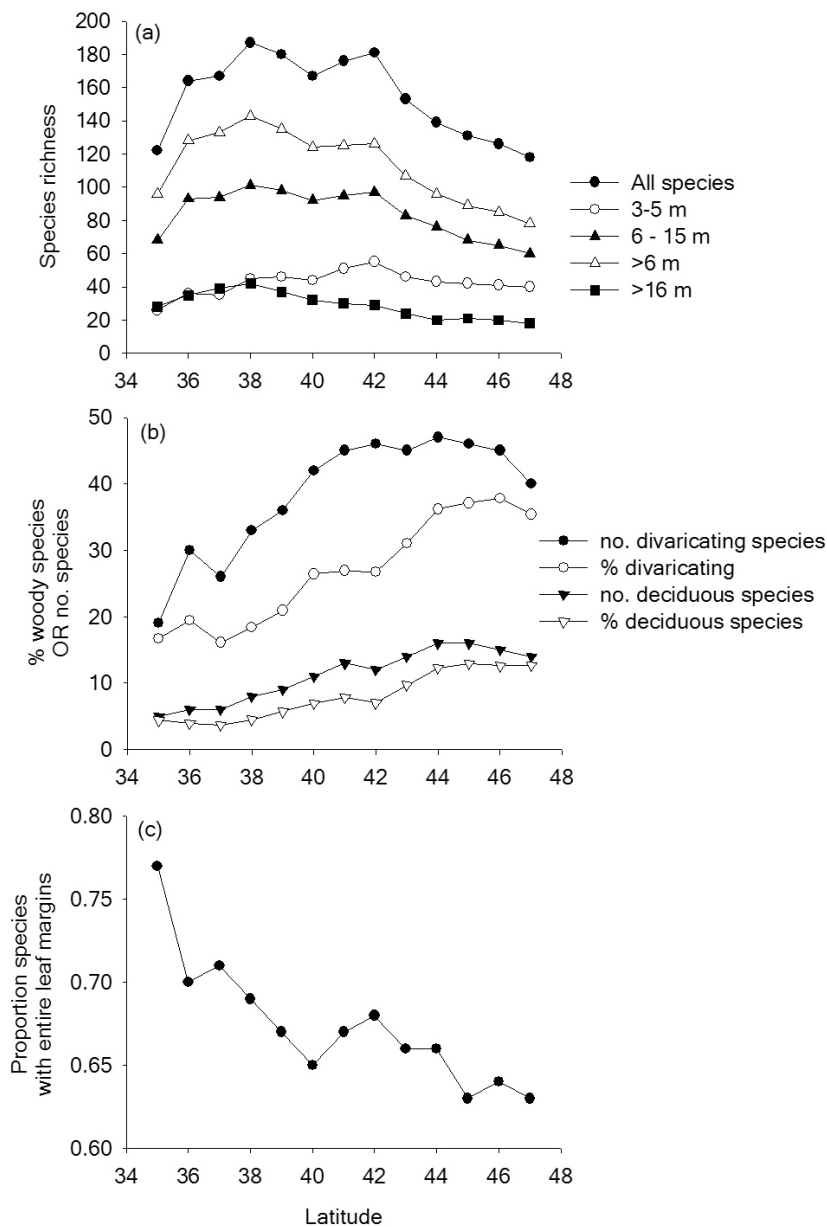


Figure 7. (a) New Zealand arborecent richness in 1° latitudinal bins. (b) Deciduous and divaricating species as a percentage of the arborecent flora in 1° latitudinal bins. (c) Species with entire-margin leaves as a percentage of the arborecent flora in 1° latitudinal bins.

annual temperature (both $r = -0.98$). A correlation between mean annual temperature and winter leaf loss is expected (McGlone et al. 2004), but not necessarily with the divaricating habit. The origin and ecological significance of the divaricating habit has been vigorously debated in New Zealand, with recent work supporting its origin as a response to moa browsing rather than climatic factors (Gibbs 2006; Lee et al. 2010). However, divaricating plants favour regions with cool winters and dry summers and thus are most abundant in the southeastern South Island (McGlone et al. 2004). Deciduous trees and shrubs also have a tendency to be divaricating (McGlone et al. 2004). The cool climate association and covariance with deciduousness ($r = 0.99$) is clearly demonstrated by our results. Regardless of the evolutionary origin of the divaricating habit, these correlations suggest the life form provides an advantage in cool, stressful environments.

International studies have shown that the proportion of woody dicotyledonous species in a local flora with entire margins has a positive linear relationship with mean annual temperature, but that the intercepts differ by biogeographic region (Kolwalski 2002; Aizen & Ezcurra 2008). Arborecents

in New Zealand with entire leaf margins are less common with increasing latitude (Fig. 7c) and have a positive correlation ($r = 0.86$) with mean annual temperature at sea level in the west within 1° latitudinal bins, similar to correlations reported elsewhere. Correlations with winter temperatures at sea level in the east ($r = 0.97$) are stronger than those with summer temperatures ($r = 0.81$) hinting that the phenomenon of toothed leaf margins is linked with cool winter and spring conditions. Leaf-margin equations developed for mid-latitude North America and east Asian floras over-predict New Zealand mean annual temperature by 7–9 °C, and those from mid-latitude Australia by 3°C. The best predictors are the leaf-margin equations for southern South America and tropical South America which over-predict by only 2.5°C.

If leaf-margin equations based on northern temperate floras are applied, arborecents in New Zealand mid-latitudes clearly belong within the subtropical zone (predicted mean annual temperature c. 20–21°C), whereas the southern South American analysis would place them in the warm temperate zone (predicted mean annual temperature c. 15–16°C). Kowalski (2002) suggests that a similar mismatch for southern South

America is a consequence of its isolation from cold-adapted northern hemisphere floras and the relatively recent (within the last 4 million years) origin of high-altitude, low temperature environments. This implies that many southern lineages have retained entire margined leaves under climate regimes that would favour toothed margins in the north, and are hence somewhat disadvantaged. However, it is equally possible that species in lineages that have evolved in northern cold temperate settings disproportionately have toothed leaves, while species derived from subtropical or tropical lineages have evolved other adaptations to cool conditions (Aizen & Ezcurra 2008). Although the deciduous habit and toothed margins are both thought to be primarily linked to cool climates, only 3 of the 11 genera that have evolved the deciduous or semi-deciduous habit within New Zealand are toothed (McGlone et al. 2004), supporting the Aizen & Ezcurra argument.

Range size of arborescents within New Zealand and Rapoport's Rule

We have calculated the mean range size for all arborescents occurring in a given 1° band (Fig. 8a). Mean latitudinal range size for New Zealand mainland arborescents is $7.2^\circ \pm 0.2$. Mean range size increases from a low of 8.6° at 36°S to 10.9° at $45\text{--}47^\circ\text{S}$. Wide-range species strongly influence the mean range size in any particular band as they occur in more latitudinal bands, which is why the lowest latitudinal band mean is higher than the overall mean. Mean range size and mean arborescent richness, excluding the three northernmost latitude bands (which have very small land areas), are negatively correlated (Fig. 8b). Correlation of individual arborescent range sizes against the southern or northern limit to their range showed a much stronger correlation with the southern limit ($r = 0.81$) than the northern limit ($r = 0.40$). That is, species are much more likely to have their ranges truncated to the south than to the north, and tree richness in the south is strongly influenced by wide-range species that extend to high latitudes. The tallest trees (≥ 25 m; $N = 22$) have wider ranges ($9.6^\circ \pm 0.8$) than the aborescent average ($6.9^\circ \pm 0.2$). Conifer arborescents are tall (mean 22.8 m ± 2.9 ; $N = 19$) with wide ranges (mean $9.6^\circ \pm 0.8$). Tree ferns have the most extensive ranges of all (mean $12.0^\circ \pm 0.4$; $N = 6$) almost certainly a consequence of the ease with which microscopic spore propagules disperse.

If dicotyledonous mainland trees alone are considered (Table 3), narrow-range trees are characteristically confined to lower latitudes, are much shorter than the mean for all dicotyledonous angiosperms, and have a low proportion of bird-dispersed fruit (0.38). Wide-range dicotyledonous trees tend to be at higher latitudes, but are not significantly taller than the mean for dicotyledonous tree species. However, they are almost twice as likely as narrow range species to have bird-dispersed fruit (0.77). Dicotyledonous tree species that occur at high latitudes are no more likely to have bird-dispersed fruit than those at low latitudes (Table 3).

Rapoport's Rule states that with increasing latitude, latitudinal range of species increases (Willig et al. 2003). Range sizes of aborescents within mainland New Zealand supports this claim (Fig. 8a). While the rule has been much debated, the most supported hypothesis is that organisms that can thrive at high latitudes can tolerate a greater range of climate regimes, and are therefore more widespread (Gaston et al. 1998). New Zealand is exceptionally well placed to test this hypothesis as, from latitude 39°S southwards, the axial mountain ranges divide the mainland into a windward wet, mild western province and a leeward drier, frosty province, which thus decouples latitude and climate variability. We use frost resistance as a proxy for

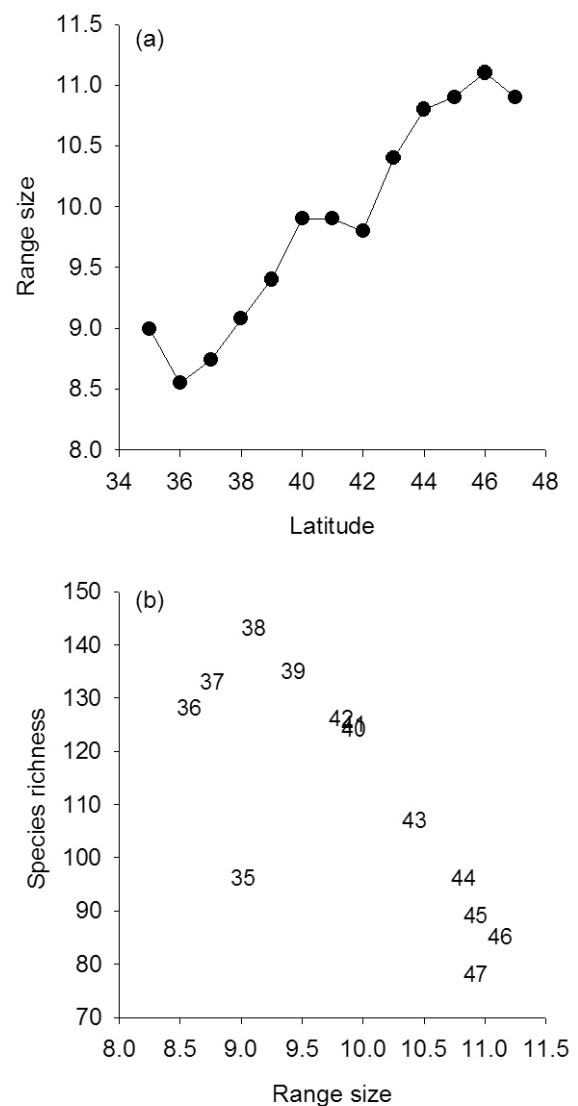


Figure 8. (a) Range size for arborescent species versus latitude. (b) Arborescent species richness versus range size. Each data point represents a 1° latitudinal bin and is given as the maximum latitude of that bin.

ability to tolerate variable climates. For the 82 arborescent species for which we have foliar frost tolerance measurements (Bannister 2003), wide-ranging aborescents ($8^\circ\text{--}13^\circ$) compared with narrow-range species ($1^\circ\text{--}5^\circ$) are more frost tolerant on average ($-7.3^\circ \pm 0.3$ versus $-4.0^\circ \pm 0.5$). However, a number of highly drought- and frost-sensitive western arborescents (e.g. *Schefflera digitata*, *Cyathea medullaris*, and *Ascarina lucida*) are among those with the largest ranges. Large ranges in New Zealand therefore do not seem to be strongly related to tolerance of cold stress.

Morin & Chuine (2006) found that tree species with larger ranges were closer to the poles, were successional seral, had small, light seeds, and short generation times. For New Zealand arborescents there is no correlation between seed mass ($r = -0.12$; $N = 162$) or seed length ($r = -0.014$; $N = 315$) and mainland range size. On the other hand, as noted above, wide-range trees are almost twice as likely as narrow-range trees to have bird-dispersed fruit and this suggests effective dispersal plays a key role in achieving or maintaining large latitudinal ranges.

Morin and Chuine's observation that seral species with short generation times may have large ranges appears substantiated: at least 80% of the 56 arborescents that range the entire New Zealand mainland can be classified as short-lived, small seral trees. These include *Aristotelia serrata*, *Coprosma robusta*, *Cordyline australis*, *Dicksonia squarrosa*, *Fuchsia excorticata*, *Griselinia littoralis*, *Leptospermum scoparium* and *Schefflera digitata*. These wide-range seral species are, without exception, abundant throughout their whole range. However, many New Zealand trees appear to be successional (although there is no widely agreed definition) and further investigation is warranted here. Tall, relatively heavy-seeded, very long-lived conifers make up most of the remaining wide-range species. A feature of New Zealand conifers is their propensity to regenerate following massive disturbance and hence their description as long-lived pioneers (Ogden & Stewart 1995).

We conclude that seral or pioneering species dispersed by birds tend to have the widest ranges – regardless of their tolerance of harsh or variable climates – and that their increasing dominance towards the south is the origin of the Rapoport's Rule correlation. We speculate that these species are better able to persist in scattered, ever-changing fragments of habitat and are then better able to repopulate areas previously over-run by glacial ice, reshaped by erosion, or made mostly unsuitable for trees by extreme glacial climates (McGlone et al. 1993).

Origins of the ecological traits of the arborescent flora

Why are there large numbers of small arborescent species in New Zealand?

Five hypotheses need to be considered with regard to selection in New Zealand for low maximum tree heights: (1) current environment; (2) selection for low heights by past (glacial) climates; (3) origin from small tree lineages; (4) selection for small sized colonists; (5) speciation within the Miocene-Pleistocene archipelago. We discuss each of these in turn.

(1) Current environments favour small trees

New Zealand spans the same latitudes as regions with the tallest trees in the world (northwest North America, Tasmania, and Gippsland, Victoria) and has similar moist, equable climates. Nor does the fertility of New Zealand soils seem to play a critical role in repressing tree growth, as tall conifer forests grow on soils of low fertility (e.g. *Dacrydium cupressinum* forests on leached terraces in Westland; and *Agathis australis* on podzolic soils in Northland). Introduced conifers and eucalypts have, in less than 150 years, achieved impressive maximum heights (*Eucalyptus saligna*, 51 m; *Pinus ponderosa* 56 m; *Sequoia sempervirens* 57 m; *Pseudotsuga menziesii*, 62 m; *Pinus radiata*, 64 m; *Eucalyptus regnans* 69 m; Burstall & Sale 1984) which exceed those of all but two indigenous trees (*Agathis australis* and *Dacrycarpus dacrydioides*). Introduced plantation conifers such as *Pseudotsuga menziesii* comprehensively outperform indigenous trees in height growth and biomass accumulation, even under droughty climates and on poor high country soils of the South Island (Benecke & Nordmeyer 1982). Given the superior performance of introduced trees over the last 150 years, and occurrence of very tall trees in similar climates elsewhere, it is difficult to believe that some as yet unrecognised aspect of the current climate or soil favours low maximum heights.

(2) Selection for small trees by cooler glacial climates

Until the late Pliocene (2–3 million years ago) New Zealand was largely forested (Mildenhall 1980). The impact of the Pleistocene glaciations (beginning c. 2.6 million years ago) was profound. The cool, often drier climates of the glaciations, accompanied by low atmospheric carbon dioxide levels, have dominated the last 2.6 million years, with conditions cooler than the present prevailing for 80% of the last 700 000 years. Up to two-thirds of the archipelago (roughly the area south of the Waikato Basin) would have been covered with scrub- and grassland-dominated communities during glacials, with forest restricted to scattered patches, sheltered or coastal sites (McGlone et al. 1993). The first major impact of the glacials appears to have been a wave of tree extinctions (Mildenhall 1980; Markgraf & McGlone 2005), although a considerable reduction of tree genera occurred earlier during the late Tertiary (Lee et al. 2001).

It could be argued that Pliocene cooling followed by cool, dry glacial climates selected against tall trees. However, as all other temperate areas suffered similar or more extreme glacial climates and concomitant extinctions (Jordan 1997), this argument does not make a case for why the New Zealand tree flora should have responded differently.

(3) Lineage and tree height

Small tree (≤ 15 m) species appear to have been recruited from lineages (originating both in New Zealand and elsewhere) covering the entire herb to tall tree spectrum. Several clades of small trees represent the maximum height attained by initially herbaceous/subshrub lineages (e.g. *Olearia*, *Hebe*, *Coriaria*, *Sophora*; Heenan et al. 2004; Wagstaff et al. 2002). Small tree lineages (e.g. *Coprosma* spp., *Dodonaea viscosa*, *Dracophyllum* spp., *Metrosideros parkinsonii*, *Myrsine* spp., *Pseudopanax* spp., *Schefflera digitata*) with both recent (Pleistocene) and relatively ancient (mid Cenozoic) residence in New Zealand (Wright et al. 2000; Mitchell & Wagstaff 2000; Mildenhall 1980) have provided many small tree species. Relatively few small trees are derived from moderately tall or tall tree lineages (e.g. *Halocarpus*, *Nestegis*, *Pittosporum*, *Podocarpus*, *Phyllocladus*, *Weinmannia*; Wagstaff 2004; Chandler et al. 2007). Many of the small to tall tree lineages appear to have been donors to the shrub or prostrate woody plant zone as well (e.g. *Lepidothamnus*, *Podocarpus*, *Pittosporum*, *Coprosma* and *Pseudopanax*).

The fact that most small tree species have small tree or subshrub/herb ancestors, suggests that phylogenetic history has contributed to the over-representation of small trees in New Zealand. However, most of the relevant lineages are well represented in other regions, but have either remained mainly as shrubs (e.g. *Olearia* in Australia) or are more species poor (e.g. *Dracophyllum*). Thus, phylogenetic constraints do not explain why these small trees have been successful in New Zealand rather than elsewhere, or why some tall tree lineages have also contributed small tree species.

(4) Transoceanic immigration selection of small trees

Many, if not all, of New Zealand trees have been derived from immigrant ancestors arriving in the course of the Cenozoic (McGlone 2006). The five tree species shared with other landmasses are short and prefer disturbed coastal situations (McGlone et al. 2001; Jordan 2001). If these are typical of the species which gave rise to the New Zealand tree flora, immigrant selection may have led to an excess of small tree species. However, this is unlikely to be a significant factor.

Some of the tallest species in the flora, for instance *Laurelia novae-zelandiae* (Renner et al. 2000); *Nothofagus fusca* (Knapp et al. 2005) appear to be derived from tall tree colonists. On the other hand, some small tree species appear to have evolved autochthonously from groups of some antiquity in the country e.g. *Coprosma* spp., *Plagianthus divaricatus* and *Podocarpus nivalis* (Mildenhall 1980). Most tree lineages have had at least 20 million years of evolution since their arrival or origin. While some tree traits might be expected to be highly conserved over such a length of time, height is not one of them. Thus, although small colonist trees from elsewhere may have contributed to the current dominance by small trees, we do not believe it is likely to be the major factor.

(5) Speciation within the Miocene–Pleistocene New Zealand archipelago

The woody lineages that have radiated extensively (more than 10 species) in New Zealand (*Carmichaelia*, *Coprosma*, *Brachyglottis*, *Dracophyllum*, *Hebe*, *Melicytus*, *Olearia*, *Pittosporum* and *Pseudopanax*) have contributed disproportionately to the aborescent flora (170/297 or almost 60%) and to the small tree component in particular (Fig. 9). The factors promoting these woody radiations (Fenner & Lee 1997) also help explain the prevalence of small arborescents.

Offshore (i.e. not connected to the mainland during low glacial sea levels) New Zealand islands are largely forested, and have therefore favoured development of woody (rather than herbaceous) endemics. Of the vascular endemics on the northern offshore islands of New Zealand, 53% are woody, that is more than twice the percentage of woody species in the flora as a whole (McGlone et al. 2001). Offshore islands lack endemic trees of tall stature; only two species, *Metrosideros kermadecensis* and *Coprosma chathamica* reach 15 m in height and overall, trees of offshore islands are somewhat shorter (mainland median = 10 m; offshore median = 9.0 m). Offshore islands have a much greater coast-to-interior ratio than the mainland, and hence exposure to persistent onshore winds. This stunts tree growth and may favour species genetically disposed to form laterally spreading canopies. Life-history aspects also favour small trees on very small islands. More

small trees can be fitted into a given space than large trees, and thus larger populations can be sustained on a limited area, potentially assisting long-term survival through maintaining genetic diversity and increasing resilience in the face of catastrophic events. In addition, successful immigrants to islands are likely to be fast maturing species or ecotypes that can exploit transient opportunities for invasion. Therefore, environment and life history factors all favour a short, fast-growing, early reproducing, multi-stemmed, wide-crowned form on small islands.

The three islands (North, South and Stewart) that make up 99% of the land area in the New Zealand region can, for biogeographic purposes, be regarded as a single landmass because they were connected during glacial low sea level stands. Offshore island groups are few and small. However, during the Oligocene and subsequently, the New Zealand landmass was split into a larger number of islands and short-lived volcanic islands formed to both the north and south. Over the late Miocene to late Pliocene (10–2 million years) tectonic subsidence affected the central regions and much of the North Island was submerged. The present northern landmass formed gradually through coalescence following uplift, especially over the last 3–0.5 million years (McGlone et al. 2001; Campbell & Hutching 2007).

We therefore suggest that over the last several million years the constantly changing archipelago of low-lying wooded islands in the northern part of New Zealand, including many short-lived volcanic landmasses, generated many locally endemic, small trees through allopatric speciation. While many tree species were doubtlessly lost as islands eroded away or were inundated, we suggest a significant number were later assimilated into the developing New Zealand landmass either through back-migration or coalescence of islands with the mainland.

While a similar generation and assimilation of island tree species would have occurred during the Oligocene inundation (c. 35–25 million years ago) and subsequent formation of the Miocene landmass (Lee et al. 2001), it appears that there has been nearly a complete turn-over of the New Zealand flora at the species level and major changes at the generic

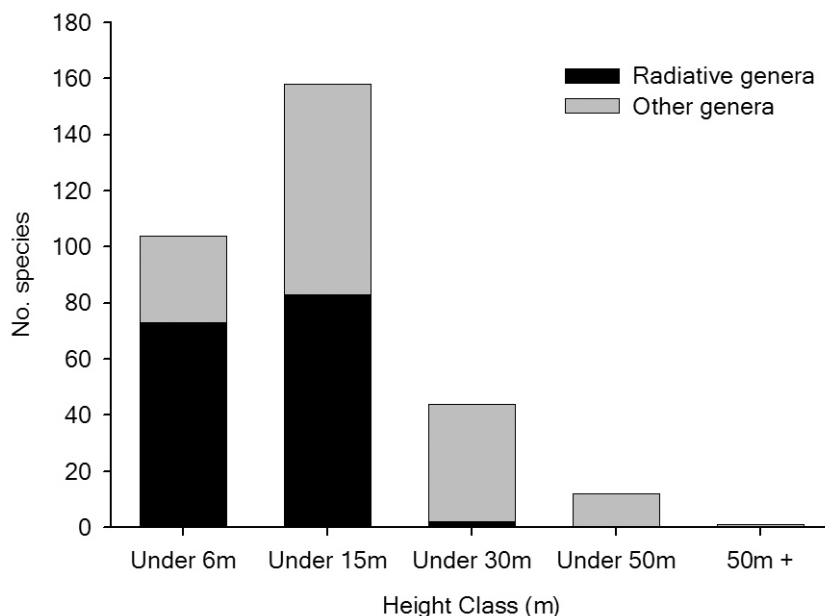


Figure 9. Number of arborescent species by height class derived from genera that have undergone significant radiation (≥ 10 spp.) and other genera that have not.

level since that time (Pole 2007a, b). Thus we suggest that the peak of this small-tree evolution, as it affects the current flora, occurred over the Pliocene and early Pleistocene, 5–0.8 million years ago.

A number of species in the small tree flora occur largely in the south (e.g. 32 *Olearia* arborescents; median mid point of range 42°S). Similar allopatric speciation may have occurred in the south as the Southern Alps formed in late Cenozoic (Winkworth et al. 2005), with isolated ranges and massifs providing disturbed, cool, windy island-like environments that favoured evolution of small trees.

We suggest that other forested archipelagos such as Hawaii, and near-archipelagos such as Florida, may have experienced similar Cenozoic allopatric speciation of small trees in the course of island formation or mountain building (see Fenner & Lee 1997).

Why have small tree species persisted in New Zealand forests?

Although allopatric speciation and immigration within the New Zealand archipelago provides a mechanism for generating small tree species, their persistence needs further explanation.

New Zealand lowland to montane forests (aside from some *Nothofagus* associations of the eastern mountain ranges of both the North and the South Island) have an abundance of small trees in the understorey and subcanopy (Wardle 1991). In the conifer–angiosperm forests that form the predominant pre-human lowland cover, the mainly conifer overstorey emerges above an angiosperm canopy, thus forming a ‘two component’ forest (Enright 1982; Ogden & Stewart 1995). The emergent conifer species only sparsely regenerate, if at all, under the angiosperm canopies, and dense regeneration is typical only after large-scale and infrequent disturbance. Lusk (2002) shows heavily stocked, early growth conifer forests are effective at reducing angiosperm biomass through dense shading. However, with aging of the emergents and their progressive failure to replace themselves, an ever-decreasing emergent overstorey of tall, old trees with diminishing leaf area eventuates, under which angiosperms can reach their potential maximum biomass. In this, New Zealand conifer forests are radically different from broadleaved northern hemisphere forests. A *Dacrydium cupressinum* stand on the west coast of New Zealand at an equivalent latitude to that of a *Quercus* spp. forest in northeastern North America, had absorbed 50% of the total radiation intercepted within the first 9 m of canopy depth and 80% by 13 m; the *Quercus* forest had absorbed the same proportion within the first 3 m and 6 m respectively (Whitehead et al. 2004).

We can generalize this model to all New Zealand forests except the most depauperate *Nothofagus* associations. First, the predominately small leaves of the major canopy and emergent trees, conifer and angiosperm alike, allow a substantial amount of photosynthetically-active radiation to reach well below them, providing a suitable light environment for small tree growth. Second, although the emergent trees necessarily take up nutrients, the competitive effect of slowly-growing, aged emergents on understorey trees is barely measurable in an old forest, and may in fact be offset by the protection they afford the subcanopy from wind and frost. Kelly (1987), in a minor classic, reports lasting effects of severe frosts on *Beilschmeidia tawa* – a moderate-sized canopy tree – and notes many reports of its increased susceptibility to damage in logged forest. The small-leaved, long-lived tall canopy and emergent trees of New Zealand may thus provide a more benign environment

for small trees than the larger-leaved canopy trees of Europe and eastern North America.

The taller canopy trees (≥ 25 m) are largely conifers (43%; 9/21) and other lineages of presumed antiquity in New Zealand (*Knightia*, *Laurelia*, *Nothofagus*). Arguably, these represent the hardy remnants of tall tree lineages of the warm temperate Miocene flora which have continued to dominate the forest overstoreys. For instance, many species of the tall, large-leaved *Nothofagus* subgenus *Brassospora*, now found in the tropics to the north of New Zealand, became extinct in New Zealand by the beginning of the Pleistocene and were replaced by the much smaller leaved *Nothofagus* subgenus *Fuscospora* species (McGlone et al. 1996). The remaining tall tree lineages have speciated little, in part because their slowness to reach maturity lengthens their generation time and possibly also because their large size reduces the possibility that they will persist as small populations. We suggest that this Miocene tall tree flora maintained its dominance in spite of depletion by extinction without replacement. Meanwhile both transoceanic migration and inter-archipelago radiation and speciation enriched the medium to small tree flora, creating the current two component emergent–canopy forest. Evolutionary transition from the small or canopy sized tree classes to the tall overstorey tree class is presumably rare. As we have seen, none of the speciose woody radiations has contributed a tree taller than 15 m. Although some shrub-small tree lineages have generated tall trees (e.g. *Sophora* and *Kunzea*), they do not act as emergents.

Why do conifers dominate in New Zealand?

Some 8% (17 species) of the mainland New Zealand tree flora consists of conifers, about one half of the percentage in the Northern temperate zone (Europe, 16.5% and North America, 16%), nearly identical to Chile (8.7%), and substantially more than our southern temperate neighbours (Victoria, 2.2%; Tasmania, 4.3%). However, while not being exceptionally speciose, New Zealand conifers have an importance out of all proportion to their species number. They are more than twice as tall as angiosperm trees (23.5 ± 2.4 m versus 11.2 ± 0.5 m) have wider ranges ($9.1^\circ \pm 1.0$ versus 7.1 ± 0.3) and dominate the biomass of many lowland to montane forests (Wardle 1991). New Zealand conifers grow approximately half as fast as their angiosperm competitors, but live much longer (Ogden & Stewart 1995). Northern temperate zone conifers favour cold winters or dry summers, nutrient-poor substrates and high frequencies of fire. Apart from fire, some New Zealand conifers are also advantaged by these environmental states, but only rarely to the exclusion of angiosperms.

New Zealand conifers differ strikingly from most northern temperate conifers in their propensity to form intimate mixtures with angiosperms in which the tall, long-lived conifer trees form an upper, often discontinuous layer (Brodribb & Feild 2008). Their persistence in an angiosperm matrix is described by the ‘lozenge model’ in which an initial catastrophic disturbance permits an intense period of conifer regeneration onto bared substrates, followed by subsequent cycles of smaller scale, mainly autogenic disturbance, in which fewer conifers manage to reach the canopy due to fern and angiosperm competition (Ogden & Stewart 1995). These semi-cyclical mixed conifer–angiosperm stands contrast strongly with boreal regions dominated by vast stands of fir, pine and larch in which angiosperms play only a minor or successional role.

The difference in conifer ecology between the temperate northern hemisphere and New Zealand may result from the

long historical development of the southern conifers under generally warm, temperate, oceanic climates. Rather than the southern conifers being relict, they may represent an evolutionary response to an evergreen forest environment under an oceanic climate regime. They dominate the tall, emergent niche by solving the problems of regeneration in the face of fast-growing fern and angiosperm competitors through specialized juveniles, adaptation to disturbance and ability to grow on suboptimal sites (Ogden & Stewart 1995).

Some of the tall (≥ 20 m) angiosperm trees that dominate the canopies and share the emergent stratum show conifer-like tendencies. Trees such as *Metrosideros umbellata*, with small, thick tough leaves and slow growth, and *Knightia excelsa* with tough, long, oblong leaves and a strikingly conifer-like, pyramidal young growth form, may be adopting a conifer-like ecology with the same disturbance-dependent regeneration strategy, as may also smaller trees such as the *Pseudopanax crassifolium* group (lancewoods) with monopodial juveniles that bear tough, narrow, very long-lived leaves. *Sophora microphylla* (height 25 m) and *Kunzea ericoides* (25–30 m) are the only species derived from small tree or shrub ancestors that have achieved tall tree status. It is interesting, therefore, that they have exceptionally small leaves and are characteristic of often dry, seral open habitat and thus have adopted a conifer-like niche.

Juvenility

The dense, often broad-leaved, small tree subcanopy characteristic of New Zealand forests poses problems for tree regeneration, especially for the slow-growing, often small-leaved dominants. About 70 arborescents have some form of marked juvenility, usually involving narrower and longer (e.g. *Elaeocarpus dentatus*), more divided or smaller leaves (e.g. *Weinmannia racemosa*), traits often associated with strongly monopodial growth forms (Dawson 1988). Among the podocarps, *Dacrycarpus dacrydioides*, *Dacrydium cupressinum* and *Prumnopitys taxifolia* have spectacular juvenile forms that give rise to drooping or small-leaved monopodial saplings. Tall *Knightia excelsa* and the smaller *Pseudopanax crassifolium*, *P. ferox* and *P. lineare* have extraordinarily elongated juvenile leaves on monopodial saplings which may lead to greater light-harvesting efficiency (Niinemets et al. 2006). Some ten broad-leaved small angiosperm trees have intensely divaricating, small-leaved, but essentially monopodial saplings (e.g. *Plagianthus regius*).

Although other explanations have been suggested (namely browsing resistance; see Lee et al. 2010), it seems worth investigating the possibility that the typically slow growth characteristic of New Zealand canopy tree juveniles (Bellingham & Richardson 2006) permits them to persist in the face of competition with vigorous, large-leaved understorey trees, much as suggested by Bond (1989) for conifers. By reducing their energy and nutrient demands, they edge slowly up through the understory by exploiting low-resource niches. Small, sparse or tough leaves and tough, long-lived stems counter climatic stress or herbivore (invertebrate and vertebrate) attack, reducing mortality. They can thus outlive and eventually overtop the shorter, faster growing broad-leaved understorey specialists.

Summary and conclusions

Compared with northern North America, Europe and southern Australia and Tasmania, New Zealand has a large number of

arborescent species relative to its land area. At a large quadrat scale ($2.5^\circ \times 2.5^\circ$ longitude/latitude) matched for net primary production, it has an arborescent richness nearly double that of North American and European quadrats. This surprising arborescent richness is largely created by small trees (≤ 15 m), most of which arose from species radiations in a few shrub and herb lineages. We suggest that these small tree species evolved in the course of the Pliocene and early Pleistocene, when New Zealand was split into numerous islands and underwent rapid mountain building. Small tree species were favoured by their rapid achievement of reproductive maturity, ability to maintain large population sizes in small areas, and tolerance of exposed conditions in both warm coastal and cool upland areas.

New Zealand, along with southeastern Australia, has a greater proportion of species with leptophyll and nanophyll leaves and lower proportion with mesophyll leaves than northern temperate floras, and a lower mean leaf width. The small-leaved nature of the New Zealand arborescent flora appears to derive from it being mostly evergreen, as, apart from dry, nutrient-poor Australia, evergreens in temperate climates elsewhere have a similar leaf size. However, unlike the situation in most temperate floras, leaf width declines with increasing height of the tree species. The emergent overstorey in New Zealand forests consists predominately of small-leaved (relative to northern hemisphere floras) angiosperms and tall conifers. We argue that small trees can persist in understoreys of forests dominated by small-leaved canopy trees, including the abundant tall conifers, as a lower proportion of light is intercepted by the canopy. The prominence of trees with marked juvenility in New Zealand forests may arise because of the need for slow-growing canopy trees to compete as juveniles in the understorey with small, large-leaved trees and shrubs.

Arborescent richness measured by 1° latitudinal bands decreases from 38°S and more sharply from 42°S . Average range size is negatively related to arborescent richness in a striking confirmation of Rapoport's Rule. New Zealand results suggest the commonly accepted explanation for wider ranges with increasing latitude (increased tolerance of climate extremes permitting wider distributions) is inadequate. Instead, it seems more likely that habitat specialists drop out with increasing latitude because of the repeated glacial–interglacial cycles which force high latitude species to undergo constant range shifts, leaving vigorous seral species dominant. Not all of these are exceptionally tolerant of climate extremes, and some, in fact, are highly sensitive, but all are adept at locating and persisting in habitat patches.

Divaricating plants, deciduous plants and plants with toothed-margin leaves all become progressively more common at high latitudes and are strongly correlated with mean annual temperature at sea level. We suggest that all of these syndromes have their origin in an evolutionary response to cool climates. However, toothed-margin leaves are much less common than in northern hemisphere sites with the same mean annual temperature and we argue this is because of the recent derivation of the New Zealand trees from evergreen, tropical to warm temperate floras.

Acknowledgments

We thank Peter Heenan, Peter Bellingham, Susan Wiser and Fiona Carswell for providing information for this study, Stephen McNeill for Figure 1, and Peter Heenan for comments on the manuscript. We are grateful to Bill Lee for a detailed and

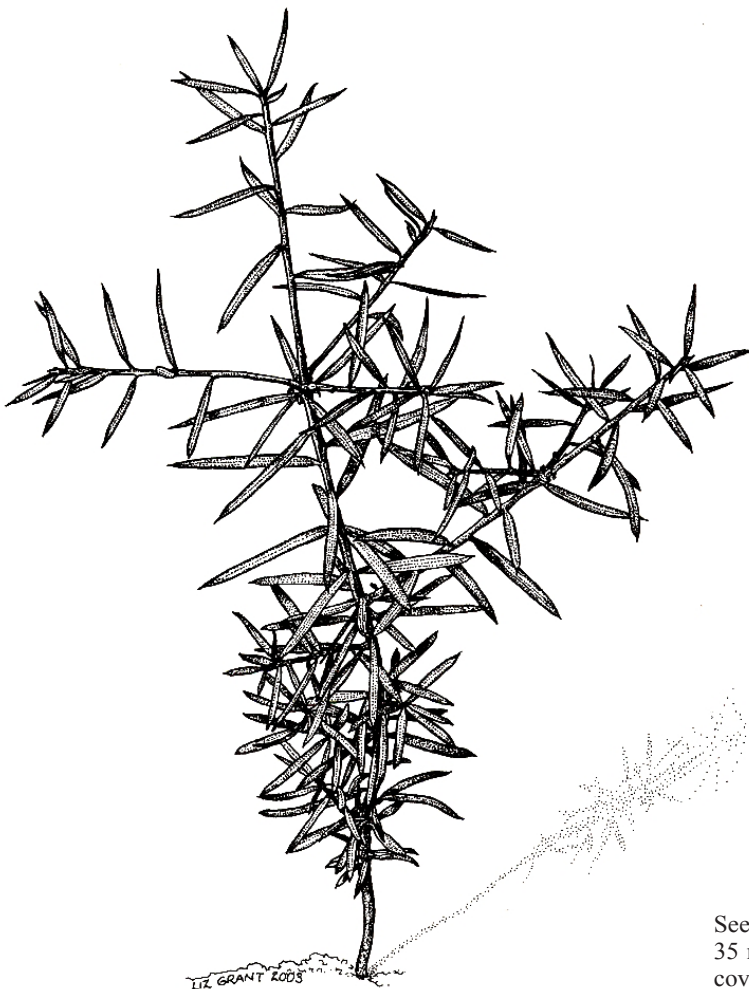
helpful critique as referee, and Dave Kelly for his extensive editorial input and Jenny Steven for technical editing. MSM and SJR contributions were funded by the Foundation for Research, Science and Technology. We thank the Department of Conservation and Landcare Research for sponsoring the publication of this special journal issue.

References

- Aarssen LW, Schamp BS, Pither J 2006. Why are there so many small plants? Implications for species coexistence. *Journal of Ecology* 94: 569–580.
- Adams JM, Woodward FI 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. *Nature* 339: 699–701.
- Aizen MA, Ezcurra C 2008. Do leaf margins of the temperate forest flora of southern South America reflect a warmer past? *Global Ecology and Biogeography* 17: 164–174.
- Allen HH 1961. *Flora of New Zealand* Vol. 1. Wellington, Government Printer. 354 p.
- Bannister P 2003. Are frost hardiness ratings useful predictors of frost damage in the field? A test using damage records from the severe frost in South Otago and Southland, New Zealand, July 1996. *New Zealand Journal of Botany* 41: 555–569.
- Bellingham PJ, Richardson SJ 2006. Tree seedling growth and survival over 6 years across different microsites in a temperate rain forest. *Canadian Journal of Forest Research* 36: 910–918.
- Bellingham PJ, Stewart GH, Allen RB 1999. Tree species richness and turnover throughout New Zealand forests. *Journal of Vegetation Science* 10: 825–832.
- Benecke U, Nordmeyer A 1982. Carbon uptake and allocation by *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole and *Pinus contorta* Douglas ex Loudon ssp. *contorta* at montane and subalpine altitudes. In: Waring RH ed. Carbon uptake and allocation in subalpine ecosystems as a key to management. Oregon, USA, Forest Research Laboratory, Oregon State University, Corvallis. Pp. 9–21.
- Bond WJ 1989. The tortoise and the hare – ecology of angiosperm dominance and gymnosperm persistence. *Biological Journal of the Linnean Society* 36: 227–249.
- Brodribb TJ, Field TS 2008. Evolutionary significance of a flat-leaved *Pinus* in Vietnamese rainforest. *New Phytologist* 178: 201–209.
- Burstall SW, Sale EV 1984. *Great Trees of New Zealand*. Wellington, AH & AW Reed (in association with NZ Forest Service).
- Campbell H, Hutching G 2007. *In Search of Ancient New Zealand*. Wellington, Penguin Books & GNS Science.
- Chandler GT, Plunkett GM, Pinney SM, Cayzer LW, Gemmill CEC 2007. Molecular and morphological agreement in Pittosporaceae: phylogenetic analysis with nuclear ITS and plastid trnL-trnF sequence data. *Australian Systematic Botany* 20: 390–401.
- Cooper AW 1960. A further application of length-width values to the determination of leaf-size classes. *Ecology* 41: 810–811.
- Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, Weston PH, Westoby M, Wilf P, Linder HP 2009. Phylogenetic biome conservation on a global scale. *Nature* 458: 754–756.
- Currie DJ, Paquin V 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* 329: 326–327.
- Curtis WM, Morris DI 1963–1975. *The Student's Flora of Tasmania*. Government Printer, Hobart.
- Dawson J 1988. *Forest vines to snow tussocks: the story of New Zealand plants*. Wellington, Victoria University Press. 264 p.
- Eagle AL 2006. *Eagle's complete trees and shrubs of New Zealand*. Vols. 1 & 2. Wellington, Te Papa Press. 1114 p.
- Elias TS 1980. *The complete trees of North America: field guide and natural history*. New York, Van Nostrand Reinhold Company. 948 p.
- Enright NJ 1982. Does *Araucaria hunsteinii* compete with its neighbour? *Australian Journal of Ecology* 7: 97–99.
- Falster DS, Westoby M 2003. Plant height and evolutionary games. *Trends in Ecology and Evolution* 18: 337–343.
- Fenner M, Lee WG 1997. A comparative study of the distribution of genus size in twenty angiosperm floras. *Biological Journal of the Linnean Society* 62: 225–237.
- Field R, O'Brien EM, Whittaker RJ 2005. Global models for predicting woody plant richness from climate: development and evaluation. *Ecology* 86: 2263–2277.
- Foreman DB, Walsh NG eds. 1993–1999. *Flora of Victoria* Vols. 1–4. Melbourne, Royal Botanic Gardens, National Herbarium of Victoria, Inkata Press.
- Gaston KJ, Blackburn TM, Spicer JI 1998. Rapoport's rule: time for an epitaph? *Trends in Ecology and Evolution* 13: 70–74.
- Gibbs GW 2006. *Ghosts of Gondwana: the history of life in New Zealand*. Nelson, New Zealand, Craig Potton Publishers. 232 p.
- Givnish TJ 1984. Leaf and canopy adaptations in tropical forests. In: Medina E, Mooney HA, Vázquez-Yanes C eds. *Physiological ecology of plants of the wet tropics*. The Hague, Dr W Junk Publishers. Pp. 51–84.
- Hall GMJ, McGlone MS 2006. Potential forest cover of New Zealand as determined by an ecosystem process model. *New Zealand Journal of Botany* 44: 211–232.
- Heenan PB, Dawson MI, Wagstaff SJ 2004. The relationship of *Sophora* sect. *Edwardsia* (Fabaceae) and *Sophora tomentosa*, the type species of the genus *Sophora*, observed from DNA sequence data and morphological characters. *Botanical Journal of the Linnean Society* 146: 439–446.
- Hitchcock CL, Cronquist A, Ownbey M, Thompson JW 1955–1969. *Vascular Plants of the Pacific Northwest*, Vols. 1–5. Seattle, University of Washington Press.
- Horn HS 1971. *The adaptive geometry of trees*. Princeton, Princeton University Press.
- Huntley B 1993. Species-richness in North-Temperate zone forests. *Journal of Biogeography* 20: 163–180.
- Jordan GJ 1997. Evidence of Pleistocene plant extinction and diversity from Regatta Point, western Tasmania, Australia. *Botanical Journal of the Linnean Society* 123: 45–71.
- Jordan GJ 2001. An investigation of long-distance dispersal based on species native to both Tasmania and New Zealand. *Australian Journal of Botany* 49: 333–340.
- Kelly D 1987. Slow recovery of *Beilschmiedia tawa* after severe frosts in inland Taranaki, New Zealand. *New Zealand Journal of Ecology* 10: 137–140.
- Kennedy EM, Spicer RA, Rees PM 2002. Quantitative palaeoclimate estimates from Late Cretaceous and Paleocene leaf floras in the northwest of the South Island, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology* 184: 321–345.

- King DA 1990. The adaptive significance of tree height. *The American Naturalist* 135: 809–828.
- Knapp M, Stöckler K, Havell D, Delsuc F, Sebastiani F, Lockhart PJ 2005. Relaxed molecular clock provides evidence for long-distance dispersal of *Nothofagus* (Southern Beech). *Public Library of Science* 3: 38–43.
- Koch GW, Sillett SC, Jennings GM, Davis SD 2004. The limits to tree height. *Nature* 428: 851–854.
- Kowalski EA. 2002. Mean annual temperature estimation based on leaf morphology: a test from tropical South America. *Palaeogeography, Palaeoclimatology, Palaeoecology* 188: 141–165.
- Lambers H, Chapin FS, Pons TL 2008. *Plant physiological ecology*. New York, Springer.
- Leathwick JR 1995. Climatic relationships of some New Zealand forest tree species. *Journal of Vegetation Science* 6: 237–248.
- Leathwick JR 2001. New Zealand's potential forest pattern as predicted from current species-environment relationships. *New Zealand Journal of Botany* 39: 447–464.
- Leathwick JR, Austin MP 2001. Competitive interactions between tree species in New Zealand's old-growth indigenous forests. *Ecology* 82: 2560–2573.
- Lee DE, Lee WG, Mortimer N 2001. Where and why have all the flowers gone? Depletion and turnover in the New Zealand Cenozoic angiosperm flora in relation to palaeogeography and climate. *Australian Journal of Botany* 49: 341–356.
- Lee WG, Wood JR, Rogers, GM 2010. Legacy of avian-dominated plant–herbivore systems in New Zealand. *New Zealand Journal of Ecology*, 34: 28–47.
- Little EL 1980. *The Audubon Society Field Guide to North American Trees*. New York, Knopf.
- Lusk CH 2002. Basal area in a New Zealand podocarp-broadleaved forest: are coniferous and angiosperm components independent? *New Zealand Journal of Botany* 40: 143–147.
- Markgraf V, McGlone MS 2005. Southern temperate ecosystem responses. In: Lovejoy TE, Hannah Leds. *Climate Change and Biodiversity*. New Haven, Yale University Press. Pp. 142–156.
- McDonald PG, Fonseca CR, Overton JM, Westoby M 2003. Leaf-size divergence along rainfall and soil-nutrient gradients: is the method of size reduction common among clades? *Functional Ecology* 17: 50–57.
- McGlone MS 1996. When history matters: scale, time, climate and tree diversity. *Global Ecology and Biogeography Letters* 5: 309–314.
- McGlone MS 2006. Becoming New Zealanders: immigration and the formation of the biota. In: Allen RB, Lee WG eds. *Biological Invasions in New Zealand*. Ecological Studies 186. Berlin Heidelberg, Springer-Verlag. Pp. 17–32.
- McGlone MS, Salinger MJ, Moar NT 1993. Palaeovegetation studies of New Zealand's climate since the Last Glacial Maximum. In: Wright HE, Kutzbach JE, Webb T III, Ruddiman WF, Street-Perrott FA, Bartlein PJ eds. *Global Climates since the Last Glacial Maximum*. University of Minnesota Press, Minneapolis. Pp. 294–317.
- McGlone MS, Mildenhall D, Pole MS 1996. History and paleoecology of New Zealand *Nothofagus* forests. In: Veblen TT, Hill RS, Read J eds. *The Ecology and Biogeography of Nothofagus Forest* New Haven, Yale University Press. Pp. 83–130.
- McGlone MS, Duncan RP, Heenan PB 2001. Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *Journal of Biogeography* 28: 199–216.
- McGlone MS, Dungan RJ, Hall GMJ, Allen RB 2004. Winter leaf loss in the New Zealand woody flora. *New Zealand Journal of Botany* 42: 1–19.
- Mildenhall DC 1980. New Zealand late Cretaceous and Cenozoic plant biogeography — a contribution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 31: 197–234.
- Mitchell AD, Wagstaff SJ 2000. Phylogeny and biogeography of the Chilean *Pseudopanax laetevirens*. *New Zealand Journal of Botany* 38: 409–414.
- Morin X, Chuine I 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distributions. *Ecology Letters* 9: 185–195.
- Niinemets U, Tobias M, Cescatti A, Sparrow A 2006. Size-dependent variation in shoot light-harvesting efficiency in shade-intolerant conifers. *International Journal of Plant Sciences* 167: 19–32.
- O'Brien EM 2006. Biological relativity to water-energy dynamics. *Journal of Biogeography* 33: 1868–1888.
- Ogden J, Stewart GH 1995. Community dynamics of the New Zealand conifers. In: Enright NJ, Hill RS eds. *Ecology of the Southern Conifers*. Melbourne, Melbourne University Press. Pp. 81–119.
- Parkhurst DF, Loucks OL 1972. Optimal leaf size in relation to environment. *Journal of Ecology* 60: 505–537.
- Pole M 2007a. Plant-macrofossil assemblages during Pliocene uplift, South Island, New Zealand. *Australian Journal of Botany* 55: 118–142.
- Pole M 2007b. Conifer and cycad distribution in the Miocene of southern New Zealand. *Australian Journal of Botany* 55: 143–164.
- Renner SS, Foreman DB, Murray D 2000. Timing transantarctic disjunctions in the Atherospermataceae (Laurales): evidence from coding and noncoding chloroplast sequences. *Systematic Biology* 49: 579–591.
- Ricklefs RE 2006. Evolutionary diversification and the origin of the diversity-environment relationship. *Ecology* 87: Suppl. S3–S13.
- Rodríguez R, Matthei O, Quezada M 1983. *Flora Arborea de Chile*. Editorial de la Universidad de Concepción. Concepción, Chile.
- Salmon JT 1980. *The native trees of New Zealand*. Wellington, Reed.
- Schuepp PH 1993. Leaf boundary layers. *New Phytologist* 125: 477–507.
- Smith AC 1979–1991. *Flora Vitiensis Nova*. Pacific Tropical Botanical Garden. Suva.
- Tissue DT, Barbour MM, Hunt JE, Turnbull MH, Griffin KL, Walcroft AS, Whitehead D 2006. Spatial and temporal scaling of intercellular CO₂ concentration in a temperate rain forest dominated by *Dacrydium cupressinum* in New Zealand. *Plant, Cell & Environment* 29: 497–510.
- Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA 1964. *Flora Europaea*. Cambridge, Cambridge at the University Press.
- Wagner WL, Herbst DR, Sohmer SH 1990. *Manual of the Flowering Plants of Hawai'i*. Vols. 1 & 2. Bishop Museum Special Publications 83. Honolulu, University of Hawaii Press, Bishop Museum Press.
- Wagstaff SJ 2004. Evolution and biography of the austral genus *Phyllocladus* (Podocarpaceae) *Journal of Biogeography* 31: 1569–1577.

- Wagstaff SJ, Bayly MJ, Garnock-Jones PJ, Albach DC 2002. Classification, Origin, and Diversification of the New Zealand Hebes (Scrophulariaceae). *Annals of the Missouri Botanical Garden* 89: 38–63.
- Wardle J 1984. *The New Zealand Beeches*. Wellington, New Zealand Forest Service.
- Wardle P 1991. *Vegetation of New Zealand*. Cambridge, Cambridge University Press.
- Webb CJ, Simpson MJA 2001. *Seeds of New Zealand: gymnosperms and dicotyledons*. Christchurch, New Zealand, Manuka Press.
- Webb LJ 1968. Environment relationships of the structural types of Australian rain forest vegetation. *Ecology* 49: 296–311.
- Whitehead D, Walcroft AS, Griffin KL, Tissue DT, Turnbull MH, Engel V, Brown KJ, Schuster WSF 2004. Scaling carbon uptake from leaves to canopies: insights from two forests with contrasting properties. In: Mencuccini M, Grace J, Moncrieff J, McNaughton KG eds. *Forests at the Land-Atmosphere Interface*. CAB International. Pp. 231–254.
- Whitham TG, Young WP, Martinsen GD, Gehring CA, Schweitzer JA, Shuster SM, Wimp GM, Fischer DG, Bailey JK, Lindroth RL, Woolbright S, Kuske CR 2003. Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology* 84: 559–573.
- Willig MR, Kaufman DM, Stevens RD 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution and Systematics* 34: 273–309.
- Wilson HD 1993. *Small-leaved shrubs of New Zealand*. Christchurch, Manuka Press.
- Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ 2005. Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Organisms, Diversity & Evolution* 5: 237–247.
- Wiser SK, Bellingham PJ, Burrows LE 2001. Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *New Zealand Journal of Ecology* 25 (2): 1–17.
- Wright SD, Yong CG, Dawson JW, Whittaker DJ, Gardner RC 2000. Riding the ice age El Niño? Pacific biogeography and evolution of *Metrosideros* subg. *Metrosideros* (Myrtaceae) inferred from nuclear ribosomal DNA. *Proceedings of the National Academy of Sciences of the United States of America* 97: 4118–4123.



Seedling of *Podocarpus totara*, a tall endemic conifer (maximum 35 m), drawn by Liz Grant (<http://www.artbyliz.co.nz/>) for the cover of *NZ J Ecology* 27(1) 2003.