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RESEARCH ARTICLE

Testing for functional convergence of temperate rainforest tree assemblages in Chile and New Zealand

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ABSTRACT

An important tenet of biogeography and comparative ecology is that disjunct assemblages in similar physical environments are functionally more similar to each other than to assemblages from other environments. Temperate rainforests in South America, New Zealand and Australia share certain physiognomic similarities, but we are not aware of any statistical evidence that these disjunct plant assemblages share a distinctive suite of functional traits, or trait combinations. We compiled height, leaf, wood and reproductive traits from the 25 commonest arborescent species at Chilean and New Zealand sites matched for summer rainfall, summer maximum temperatures, and winter minimum temperatures. We then used multivariate tests of trait convergence. Tropical and subtropical assemblages served as out-groups. PERMANOVA showed convergence of trait centroids at the two temperate sites, where trees on average had denser wood and smaller leaves than trees at the (sub)tropical sites. Principal components analyses carried out separately on each assemblage showed that the Chilean and New Zealand assemblages were also the most similar pair in terms of trait relationships, although New Zealand also shared strong similarities with subtropical Argentina. The main axis of variation in both temperate assemblages ranged from small, short-lived understorey trees with soft leaves, to emergents with sclerophyllous leaves and fairly dense wood. However, the New Zealand assemblage was much richer in small trees with soft leaves than its Chilean counterpart; possible historical influences on this difference include conditions favouring radiation of small trees during the late Neogene in New Zealand, competition from *Chusquea* bamboos in Chile and the historical absence of browsing mammals from New Zealand. Environmental filtering has produced similar values of individual traits in Chile and New Zealand, but only partial convergence of functional trait combinations. As far as we know, this is the first study to statistically test whether disjunct tree assemblages on climatically matched sites are more functionally similar to each other than to assemblages from other environments.

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Introduction

The idea of convergent evolution in similar but disjunct environments was traced by Cody and Mooney (1978) to influential publications by Schimper (1902) and Warming (1909). The vegetation of Mediterranean ecosystems has been something of a poster child for convergent evolution, beginning with Schimper's observation that Mediterranean climates on far-flung continents were home to similar sclerophyllous woody plants that were not necessarily closely related. Much work has since explored physiognomic and functional similarities and dissimilarities between the vegetation of the Mediterranean basin, California, Chile, the Cape region of South Africa and southwestern Australia (e.g. Cody & Mooney 1978; Cowling & Witkowski 1994; Arroyo et al. 1995; Cowling et al. 2005). However, there is little if any statistical evidence that these disjunct plant assemblages share a distinctive suite of traits, or of functional types, that can be considered uniquely 'Mediterranean'. For example, Barbour and Minnich (1990) noted that chaparral-type vegetation in North America extends well beyond the limits of the Mediterranean climate of California.

Temperate rainforests occur, like Mediterranean woodlands, on widely separated landmasses in both hemispheres. Temperate rainforests in South America, New Zealand and southeastern Australia share some basic structural and functional similarities in the dominance of evergreens, and a complex vertical structure including large emergent trees that, at least on lowland sites, appear to depend mainly on coarse-scale disturbance for regeneration (Enright & Hill 1995; Veblen et al. 2016). Less evident shared features include floristically and functionally diverse epiphyte communities (Taylor et al. 2016), and predominance of arbuscular mycorrhizal associations (Johnson 1977; Godoy et al. 1994) and of avian seed dispersal (Read & Hill 1983; Armesto & Rozzi 1989; Clout & Hay 1989), but none of these is unique to temperate rainforests. Dissimilarities between these different regions are also readily apparent. Understoreys and tree-fall gaps are dominated by tree ferns in New Zealand and temperate Australia (Wardle 1991; Ough & Murphy 1996), but in South America their place is taken by *Chusquea* bamboos (Veblen et al. 1996b). New Zealand is richer in conifers than either of the other two regions (Enright & Hill 1995), and also richer in small trees (< 15 m tall) (McGlone et al. 2010).

Despite the gross overall similarities outlined above, it is not known if temperate rainforest assemblages in South America, New Zealand and Australia share a distinctive suite of functional traits, or trait combinations. The occurrence of similar present-day environments is far from a sufficient condition for functional convergence, as the degree to which convergence will be realized depends on how well several other conditions are met (Cody & Mooney 1978). These include similar antiquity of the present-day environments on the different landmasses, availability of organisms with the genetic potential to produce similar phenotypes, and a lack of confounding historical and chance effects. It is questionable whether these conditions are well satisfied when we compare temperate rainforests on the different southern landmasses (Lee et al. 2016). For example, although tree ferns are well-represented in the Palaeogene fossil record of southern South America (Barreda 1997; Barreda et al. 2009), their subsequent ousting from forest understoreys by fast-growing *Chusquea* bamboos may have altered the fitness landscapes of woody plants. The tall species of *Chusquea* found in the lowland forests of temperate South America pose a formidable obstacle to regeneration of tree species (Veblen et al. 1996b; González

et al. 2002), without offering the opportunities for epiphytic establishment afforded by tree fern stems in New Zealand and elsewhere (Oliver 1930; Newton & Healey 1989; Beveridge 1973).

Here we test for functional convergence of temperate rainforest tree assemblages at a pair of climatically matched sites in South America and New Zealand, using subtropical and tropical forest assemblages in Argentina and Bolivia as out-groups. Previous comparisons of functional traits across different regions with similar climates have usually focused on univariate comparisons of means or ranges of trait values (e.g. Cody & Mooney 1978; Cowling & Witkowski 1994; Smith 1996; McGlone et al. 2010). It is also useful to ask whether trait relationships differ between assemblages, as variation in seasonality, disturbance regimens and other environmental factors could influence the range of viable trait combinations (Loehle 2000; Lamanna et al. 2014). For example, tall fast-growing tree species that regenerate in tree-fall gaps are common in tropical and subtropical rainforests, but few are found at higher latitudes; this probably reflects the influence of solar elevation angles on light availability in tree-fall gaps (Lusk et al. 2011). Accordingly, in addition to comparing the means and multivariate centroids of trait distributions at the different sites, we also ask whether the combinations of height, wood, leaf and reproductive traits found in the two temperate assemblages resemble each other more than they do those of the tropical and subtropical assemblages.

Materials and methods

Study site selection

To compare climates in the two temperate regions, we obtained temperature and precipitation data from 71 New Zealand sites and 35 South American sites (Appendix 1) that currently support temperate forest vegetation, albeit reduced to small remnants on many lowland sites (Hajek & Di Castri 1975; Dirección Meteorológica de Chile 2001; NIWA 2015). Climate data were obtained from a similar range of latitude (c. 37 to 47°S) in both regions; New Zealand sites from Auckland northwards were excluded, as the warm, moist conditions found throughout most of this northernmost region of the country have no close analogues in Chile or Argentina.

Our site-matching procedure aimed to maximize similarity in terms of the bioclimatic variables (Nix 1986; Busby 1991) of most importance for plant physiology. It is very difficult to find Chilean and New Zealand temperate forest sites with exactly the same monthly combinations of temperature and precipitation. Most sites in temperate South America have rainy winters and relatively dry summers (di Castri & Hajek 1976), rainfall during the warmest quarter on average contributing only 12% (range 5%–24%; Appendix 1) of mean annual precipitation across the 35 South American sites in our data set. Precipitation is much less seasonal on average in New Zealand, where an average of 23% falls during the warmest quarter (range 17%–36%). For the present purpose of comparison between regions that differ in the seasonality of precipitation, we argue that precipitation during the warmest months of the year is far more relevant to plant physiology than mean annual precipitation; summer precipitation, in combination with summer maximum temperatures, will determine the highest level of drought stress to which plants are exposed. In a similar vein, we argue that mean daily minimum temperatures during

winter are more informative than mean annual temperatures, because they indicate the level of cold stress that plants encounter. We therefore used just three bioclimatic variables to compare South American and New Zealand sites: (1) rainfall during the warmest quarter, (2) mean daily maxima of the warmest month, and (3) mean daily minima of the coldest month. Although diurnal temperature range is another widely used variable of potential relevance to plant physiology, in our data set of 106 sites it was found to be highly collinear ($r = 0.94$) with annual temperature range (variable 2–variable 3); it was therefore omitted from our analysis.

Principal components analysis (PCA) of the three climatic variables was used to determine overall similarity of sites in the two regions (Figure 1). The first two axes extracted accounted for 47% and 33% of the variance. The first (horizontal) axis corresponds to a gradient of summer drought stress; sites with warm, dry summers scoring low, and those with cool, moist summers scoring high. The second axis represents winter minimum temperatures. As the author responsible for obtaining traits of the South American temperate assemblage had access to a well-conserved and extensive forest remnant near Valdivia, we sought an equivalent site in New Zealand; PCA identified Palmerston North as the closest match (Table 2). Both sites are located on alluvial terraces beside major rivers.

Consistencies in the distribution of forest types across the first two dimensions of our PCA suggested that we chose climatic variables that were highly relevant to tree species sorting. Although we did not formally analyse climate–vegetation relationships, forest types in both Chile and New Zealand were fairly homogeneous across the upper left quadrant containing our two study sites (Figure 1). In Chile, this quadrant corresponds closely to the climatic envelope of forests dominated by the deciduous *Nothofagus obliqua* (syn. *Lophozonia obliqua*) and the broadleaved evergreens *Persea lingue* (Lauraceae), *Laurelia sempervirens* (Atherospermataceae) and *Aextoxicon punctatum* (Aextoxicaceae) (Veblen & Schlegel 1982). In New Zealand, this combination of warm, relatively dry summers and mild winters is the domain of lowland podocarp-broadleaved forest lacking *Nothofagaceae*. Although the podocarps *Dacrycarpus dacrydioides*, *Prumnopitys taxifolia* and *Podocarpus totara* usually dominate the upper storey, the tree species most closely associated with this climatic envelope are probably the broadleaved evergreen *Alectryon excelsus* (Sapindaceae), and to a lesser extent *Laurelia novae-zelandiae* (Atherospermataceae) and *Beilschmiedia tawa* (Lauraceae) (Leathwick 2001). *Alectryon excelsus* in fact formed most of the forest canopy at our study site near Palmerston North (Atkinson & Greenwood 1972).

Two semi-deciduous, humid forest assemblages from different climates were used as out-groups for our comparison of the two temperate assemblages. A subtropical forest assemblage was sampled at San Javier in northwestern Argentina, building on existing data gathered by Easdale and Healey (2009). Detailed climate data were not available from the study area itself, located in hill country about 15 km west of the nearest meteorological station in the city of San Miguel de Tucumán (Table 1). In contrast to the two temperate sites, rainfall at Tucumán is highest during summer and lowest in winter, with only 40 mm falling during the winter quarter. As the study area is 100–500 m higher in elevation than San Miguel de Tucumán, temperatures will be cooler, and rainfall higher, than the figures given in Table 1. This expectation is confirmed by a single year's measurements in the study area by Hunzinger (1997), giving a rainfall of 1262 mm (275 mm during the winter quarter) supplemented by 156 mm from fog (123 mm during the

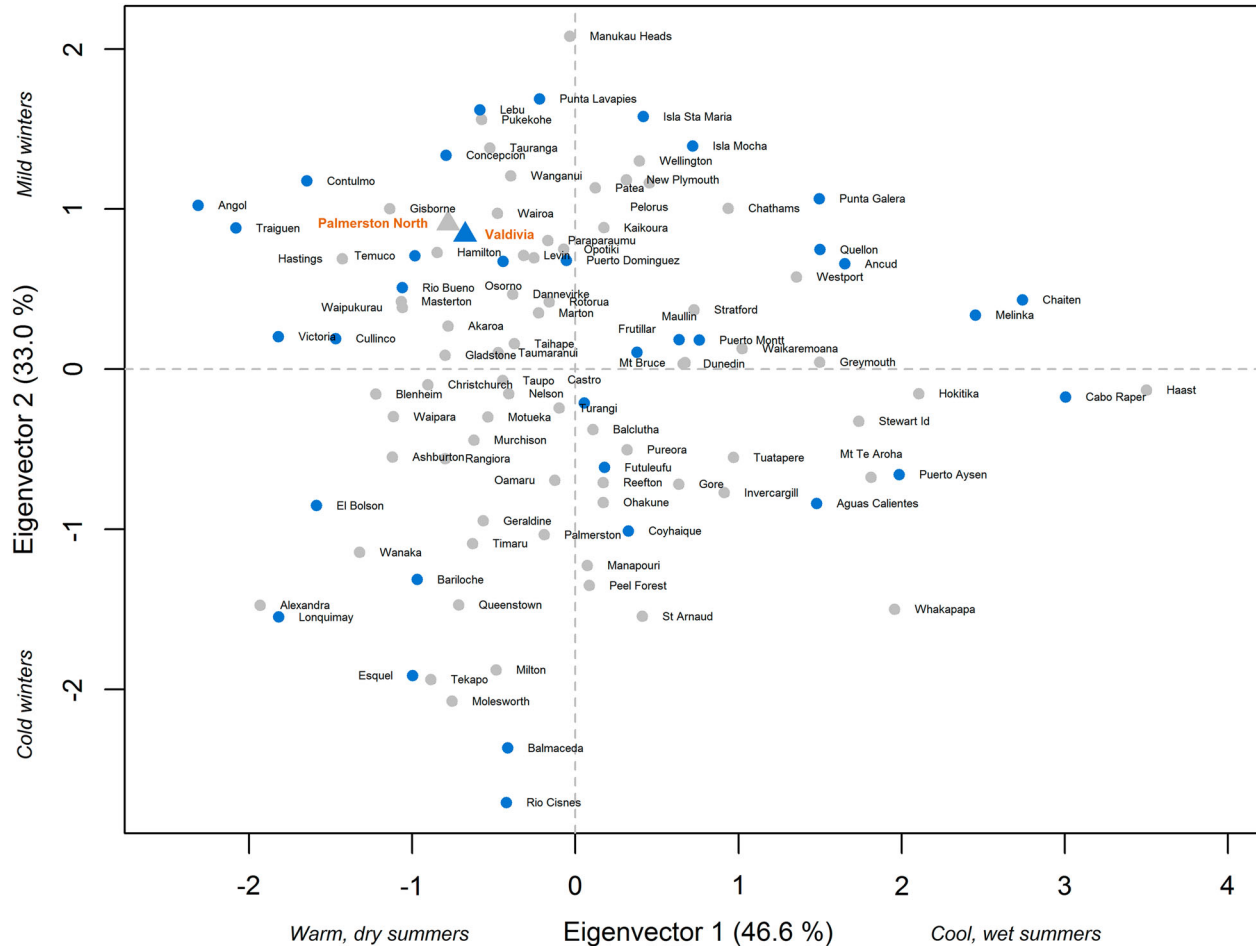


Figure 1. Principle components analysis of bioclimatic variables of temperate forest sites in New Zealand (grey) and temperate South America (blue). Large triangular symbols with orange labels highlight the two study sites at which tree functional traits were sampled. The first axis is positively correlated with rainfall during the warmest quarter ($r = 0.83$), and negatively with mean daily maximum temperatures of the warmest month ($r = -0.82$). The second axis corresponds to mean daily minima of the coldest month ($r = 0.98$).

Table 1. Geographic location of study sites and climatic statistics from nearest meteorological stations.

Site	Country	Grid reference	Elevation (m)	MAT (°C)	Mean annual precipitation (mm)	Mean daily max. warmest month (°C)	Mean daily min. coldest month (°C)	Precipitation of warmest quarter (mm)
Palmerston North	New Zealand	40°21'S, 175°37'E	46	13.1	918	23.5	4.6	175
Valdivia	Chile	39°49'S, 73°15'W	5	12.9	1788	22.9	4.5	160
San Miguel de Tucumán	Argentina	26°47'S 65°23'W	480	19.5	1109	30.4	19.8	595
La Chonta	Bolivia	15°47'S, 62°55'W	400–500	24.0	1580	–	–	–

Sources: Hajek and Di Castri (1975), Dirección Meteorológica de Chile (2001), Peña-Claros et al. (2008), NIWA (2015), Estación Experimental Obispo Colombres, unpublished data. Data from La Chonta are incomplete.

winter quarter). Data were also obtained from a well-studied tropical forest assemblage at La Chonta in Bolivia, one of the authors (LP) adding new unpublished data to existing data taken from Poorter and Rozendaal (2008) and Poorter et al. (2010). Mean annual temperature and mean annual rainfall area were the only climate data available for La Chonta, which also experiences a dry season during the cooler months, although only during July does evapotranspiration exceed rainfall (Peña-Claros et al. 2008).

Stand and species selection

We sampled the 25 most abundant tree and large shrub species (as assessed by visual estimates of percentage cover) in the best-conserved forest remnant in the vicinity of each of the two temperate sites. These were Bosque San Martin, 15 km north of Valdivia, and Keebles Bush, 5 km southwest of Palmerston North. Both these forest remnants lie on alluvial terraces, as do the meteorological stations where climatic data were captured (Table 1). As we were not authorized to sample leaf or wood traits at Keebles Bush, the 25 species recorded as the commonest species there were sampled at other smaller forest remnants nearby, chiefly Kahuterawa Bush on land owned by the New Zealand Defence Forces.

Data were also obtained from 25 tree species at each of the two out-group sites. These were all species reported as locally common (Peña-Claros et al. 2008; Poorter & Rozendaal 2008; Easdale & Healey 2009; Poorter et al. 2010). However, one or more of the traits we wished to include in our analysis were not available for some of the most abundant species at La Chonta (e.g. *Pseudolmedia laevis*, *Ampelocera ruizii*) so we cannot claim to have included the 25 most abundant species at that site.

Trait selection

We aimed to include as many independent dimensions of ecological significance as possible (Table 2). By ecological significance we mean that there must be evidence that the trait in question is related to 'how the species makes a living or where it does best' (Westoby et al. 2002). Our other two selection criteria were that the trait be easy to measure accurately, and readily expressed as a quantitative variable. Most of the chosen traits are in regular use in plant ecology and ecophysiology (Table 2).

The leaf economics spectrum is widely accepted as a major axis of variation relevant to ecological differences between plants (Westoby et al. 2002; Wright et al. 2004). Leaf dry mass per area (LMA) is the easiest to measure of this suite of traits, but suffers from two important drawbacks. First, the highly plastic response of LMA to light environment (Wilson et al. 1999; Poorter et al. 2009) makes standardization of sampling environments critical, but it is not always feasible to find all species in a common light environment. Second, LMA is difficult to apply to scale-leaved conifers, two of which were present in our data set. We therefore opted to instead measure leaf dry matter content (LDMC), which is less sensitive to light environment (Lusk et al. 2010), and readily applicable to non-laminar leaves. Although LDMC correlates well overall with LMA across a large data set (Wilson et al. 1999), it did not distinguish clearly between deciduous and evergreen leaves in our data set; we therefore included leaf habit as an additional variable, recognizing three character states: evergreen, semi-deciduous and deciduous. At the subtropical site, this distinction was based on measurements of leaf retention during the dry

Table 2. Traits used to characterize functional variation within tree assemblages at humid forest sites in New Zealand, Chile, Argentina and Bolivia, and evidence for their ecological significance.

Trait	Character states/ units	Reported evidence for ecological significance	
		Distributional correlates	Functional correlates
Final height ¹	m	Latitude (–), precipitation (+) (Moles et al. 2009).	Determines hierarchical access to light (Falster & Westoby 2003). Sometimes correlated with longevity (+) and growth rate (–)(Loehle 1988; Falster & Westoby 2005), but not always (Easdale & Healey 2009).
Twig wood density	g cm ^{–3}	Precipitation (–) (Chave et al. 2006), soil fertility (–) (Muller-Landau 2004). Wider variation at low latitudes and elevations (Swenson & Enquist 2007).	Correlated with juvenile growth rate of seedlings and saplings (–), survival (+), longevity (+), stem resistance to breakage (+), and tolerances of shade and drought (+) (e.g. Hacke et al. 2001; van Gelder et al. 2006; Poorter et al. 2010; Wright et al. 2010).
Leaf habit ²	0 = deciduous, 1 = semi-deciduous, 2 = evergreen	Seasonality (Kikuzawa 1991), soil fertility (Monk 1966).	Correlated with nutrient loss rates (Escudero et al. 1992).
Leaf dry matter content	%	Soil fertility (–) (Hodgson et al. 2011).	Correlated with leaf toughness and lifespan (+), growth rate (–), shade tolerance (+), attractiveness of foliage to herbivores (–) (Kitajima & Poorter 2010; Lusk et al. 2010).
(log) Leaf size (area)	mm ²	Site water balance (+) (Peppe et al. 2011). Temperature (+) and soil fertility (+) in humid forests (Webb 1968).	Influences susceptibility to radiative overheating and chilling (Parkhurst & Loucks 1972; Leuning & Cremer 1988). Influences efficiency of foliage display in juveniles (+) (Lusk et al. 2012), and likelihood of herbivore damage (+) (Moles & Westoby 2000; Pollock et al. 2007).
(log) Seed mass	Mg	Latitude (–) (Lord et al. 1997).	Correlated (+) with seedling survival of hazards such as drought, shade, and litter (Moles & Westoby 2004).
Pollination syndrome ³	0 = wind, 1 = biotic	Latitude (Whitehead 1969; Willson et al. 1989).	

¹Sources: Poole and Adams (1990), Armesto et al. (2011), Grubb et al. (2013), Hoffmann (1997), Easdale and Healey (2009), Poorter et al. (2010).

²Sources: Armesto et al. (2011), Easdale and Healey (2009), L. Poorter, unpublished data.

³Sources: Newstrom and Robertson (2005), Easdale et al. (2007), Norton (1984), Otegui and Cocucci (1999), de Oliveira Barros (2013), Yamamoto et al. (2007), Bush and Rivera (2001).

season (Easdale & Healey 2009): species retaining > 50% of foliage during the dry season were classed as evergreen, those retaining 10%–49% were classed as semi-deciduous, and those with < 10% foliage retention were regarded as deciduous. Leaf habit was assessed subjectively at the Bolivian site, and was based on published species descriptions in New Zealand and Chile (Table 2).

Despite recent touting of a ‘whole-plant economics spectrum’ embracing leaf, stem and root traits (Reich 2014), we thought it also useful to include wood density as another major dimension of ecological variation, in addition to LDMC. The relationship of wood density with leaf economics remains controversial, a major study of tropical trees finding leaf and stem economic traits to be orthogonal (Baraloto et al. 2010). However, that study used specific leaf area and leaf tissue density as measures of leaf economics, not LDMC.

Pollination syndromes were also included as a binary variable: wind versus biotic. Reproductive traits tend to be under-studied in comparative ecology, but the

representation of different pollination and seed dispersal syndromes in plant assemblages varies along environmental gradients (Whitehead 1969; Willson et al. 1989), suggesting that environment differentially influences the viability of different character states of these traits. Although a great variety of pollination syndromes have been described, they can also be usefully reduced to a binary variable (wind versus biotic) that is tractable in multivariate analyses. However, the diversity of seed dispersal syndromes found in humid forests is less susceptible to expression as a binary or ordinal variable; dispersal syndromes were therefore not included.

Trait sampling

Leaf size, LDMC and wood density were calculated from tissues obtained from five replicate saplings (1–3 m tall) of each species, or from low branches of taller trees if saplings were scarce or absent. We aimed to avoid sampling individuals growing in extreme light environments, i.e. very exposed north-facing forest margins and deep shade. Four to 42 leaves or leaflets were obtained per plant, depending on leaf size. Leaves were placed immediately in re-sealable plastic bags with moist paper, and blotted dry before determining fresh weight and area; they were then oven-dried at 60 °C for 3 days; in the case of species with compound leaves, the area and mass of leaflets was measured, rather than whole leaves (Cornelissen et al. 2003). Petioles and petiolules were not removed from laminae before determination of area and LDMC. Leaf area was measured using an LI-3100 Area Meter (Li-Cor).

A 60–120 mm long section of twig (6–10 mm diameter) from each plant was used to estimate wood density. Volume of the section was estimated by measuring (a) the length, and (b) the diameter on two orthogonal axes, at three points along the length of the section. Bark and phloem were stripped before measuring stem volume in New Zealand, Chile and Argentina, but not in Bolivia. Samples were then oven-dried for 3 days at 60 °C before determining dry weight. Data from the Bolivian tropical site show that twig wood densities average about 25% lower than densities of cores from the trunk, but that the two measures are strongly positively correlated ($r = 0.79$).

Height, leaf habit, seed mass and pollination syndrome were obtained from published sources (Table 2).

Statistical analyses

We used analysis of variance (ANOVA) to test for significant effect of region on means for continuous traits, with Tukey's honest significant difference as a post-hoc test for significant pairwise differences between regions. A \log_{10} transformation was applied to leaf size and seed mass for ANOVA. We used chi-squared tests for equal proportions to test for an overall effect of region on pollination syndrome and leaf habit, and binomial tests for pairwise comparisons between regions for each pollination syndrome and leaf habit class. PERMANOVA was used to test for significant differences between regions for all traits simultaneously. We conducted PERMANOVA across all regions, and to all pairwise combinations of regions. In all PERMANOVA analyses we used Gower's distance as our dissimilarity measure and 1000 permutations. These analyses were carried out in R (R Development Core Team 2008). A PCA, carried out in PC-ORD (McCune & Mefford

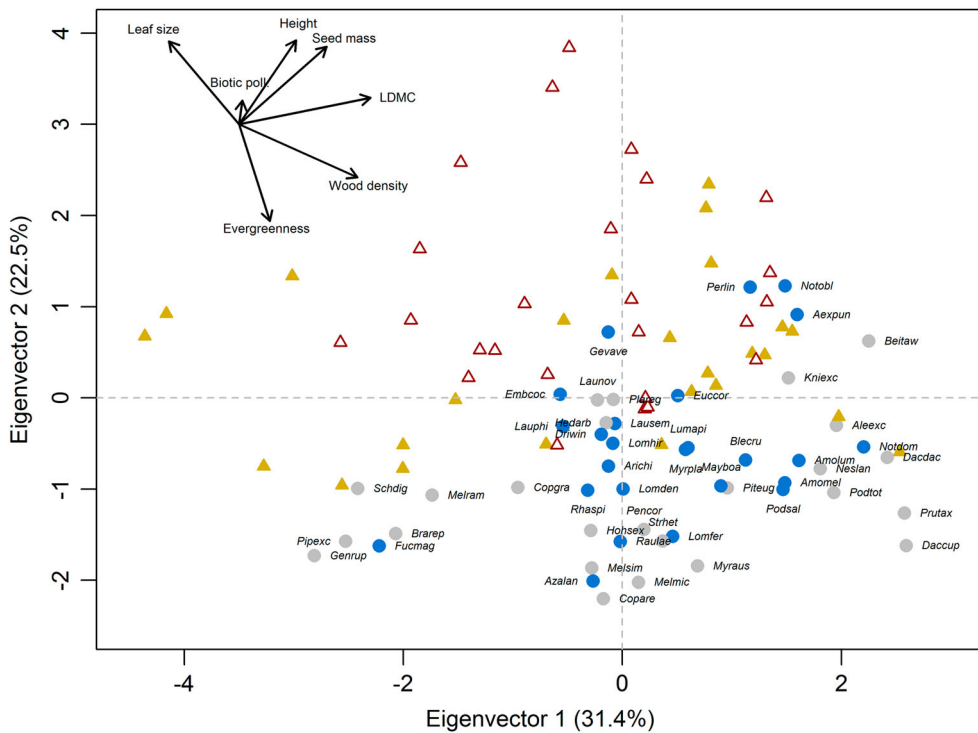


Figure 2. Combined principal components analysis of functional traits of four humid forest tree assemblages. Grey dots show (temperate) New Zealand species, blue dots show (temperate) Chilean species, gold triangles show (subtropical) Argentine species, red triangles show (tropical) Bolivian species. Six-letter species codes (see Appendix 1 for full names) are given only for the two temperate assemblages, to avoid clutter. Arrows show loadings of traits on the first two axes. Axis one is associated most strongly with leaf dry matter content (Kendall's $\tau = 0.72$) and wood density ($\tau = 0.57$). Axis two is associated mainly with evergreenness ($\tau = -0.49$), final height ($\tau = 0.48$), and leaf size ($\tau = 0.38$).

2011), was used to visually summarize overall functional differences and similarities among the four assemblages (Figure 2). Four separate PCAs were used to identify loadings of traits on the first two axes of variation in each assemblage, and used trait loadings on the first two axes to compare trait relationships at the four sites. As leaf habit was expressed as an ordinal variables with three levels (deciduous, semi-deciduous, evergreen), we used Kendall's tau as our measure of association, rather than the Pearson correlation coefficient.

Results

Trait means

PERMANOVA showed that, on average, species from the two temperate forest assemblages resembled each other closely, but differed significantly from those at the subtropical and tropical sites (Table 3). This pattern is approximated visually by the ordination of species from the four assemblages on the first two axes of a combined PCA (Figure 2). The individual traits that differed most consistently between temperate and non-temperate sites were wood density and proportion of evergreen species, both of which were significantly higher on average at the temperate sites (Figures 3, 4). This difference in mean

Table 3. PERMANOVA comparing trait centroids of tree assemblages in four humid forest: two temperate (New Zealand, Chile), one subtropical (Argentina) and one tropical (Bolivia).

Assemblages compared	F. Model	R ²	P-value
All	7.3	0.19	0.001
New Zealand vs. Chile	1.6	0.03	0.200
New Zealand vs. Argentina	10.4	0.18	0.001
New Zealand vs. Bolivia	11.0	0.19	0.001
Chile vs. Argentina	8.5	0.15	0.001
Chile vs. Bolivia	5.8	0.11	0.002
Argentina vs. Bolivia	2.9	0.06	0.036

wood density reflects a wider range of values in the non-temperate assemblages: maximum values were relatively similar at all four sites, but the subtropical and tropical assemblages included species with wood densities of $< 0.3 \text{ g cm}^3$, lower than anything found at either of the two temperate sites (Figures 3, 5A). Although leaves and seeds both tended to be smallest in New Zealand and Chile, they were not significantly larger at the subtropical Argentine site (Figure 3). Microphylls were the dominant leaf size class at the New Zealand, Chilean and Argentine sites, whereas mesophylls (sensu Webb 1959) were typical of the Bolivian assemblage. There were no significant differences between sites in the probability of wind pollination, which accounted for between three and five species at all sites, i.e. only 12%–20% of species were wind-pollinated.

Relationships among traits

The common thread among all four assemblages was a strong loading of LDMC and wood density on the first PCA axis (Table 4). The association of LDMC and wood density is confirmed by significant positive correlations between these two variables in all assemblages except Chile (Figure 5D). The number and identities of other traits associated with axis one varied across the four assemblages. The only commonality in trait loadings on axis two was the dominance of leaf habit on that axis in both non-temperate assemblages (Table 4). Correlation matrices are included in Appendix 1.

The Chilean and New Zealand assemblages were the most similar pair in terms of trait relationships (Table 5). There was a significant positive correlation between trait loadings of these two temperate assemblages on the first PCA axis ($r = 0.81$, $P = 0.027$). However, trait loadings of the New Zealand assemblage on axis 1 were also significantly positively correlated with those of the Argentine assemblage ($r = 0.78$, $P = 0.039$). The New Zealand, Chilean and Argentine assemblages shared similar strong loadings of height and LDMC on axis one: at all three sites, tall trees tended to have sclerophyllous leaves, and small trees mostly had soft leaves (Table 4; Figure 5B). The only other significant correlation between the trait loadings of assemblages (Table 5) was that of Argentina versus Bolivia on PCA axis 2 ($r = 0.94$, $P = 0.0016$).

Two differences between the two temperate assemblages were apparent. First, despite similar positive relationships of LDMC with height, the New Zealand assemblage was much richer in small trees with soft leaves, including nine species $< 15 \text{ m}$ tall having LDMC $< 30\%$, compared with only two in Chile (Figure 5B). Second, leaf size showed a strongly significant negative relationship with tree height in New Zealand, but no significant relationship in Chile (Table 4; Figure 5C).

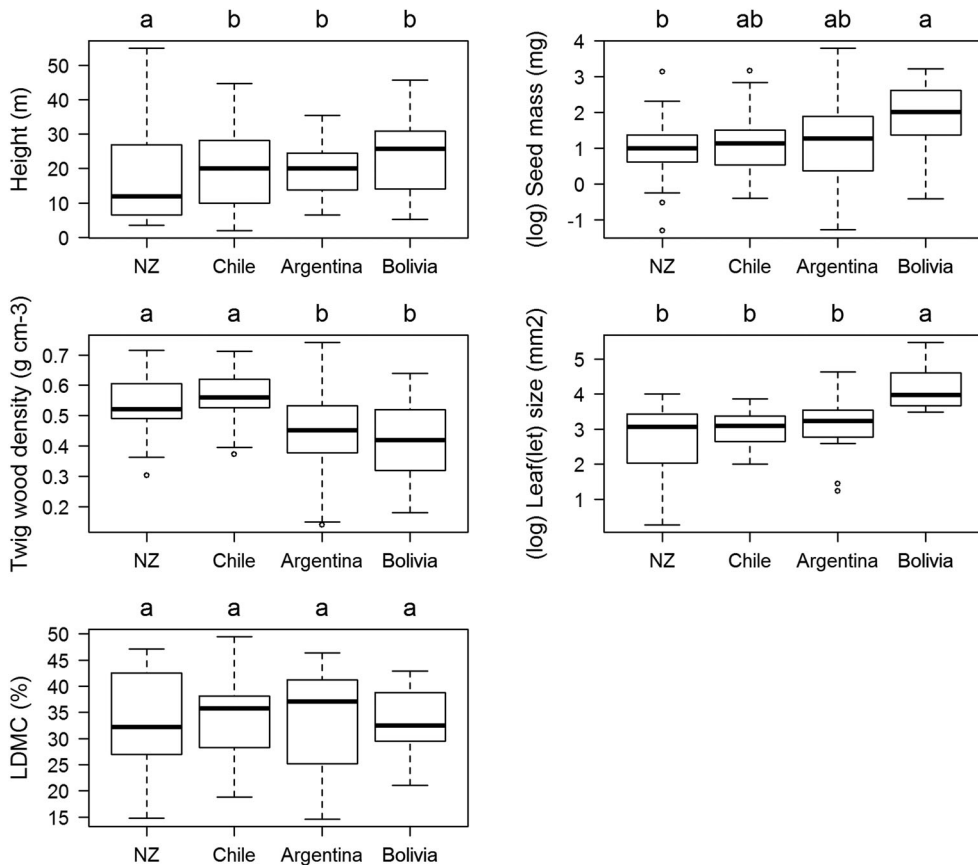


Figure 3. Comparisons of functional traits in four humid forest tree assemblages: two temperate (New Zealand, Chile), one subtropical (Argentina) and one tropical (Bolivia). All traits expressible as continuous variables are shown here. Means sharing the same letter do not differ significantly at $P = 0.05$ (Tukey's honest significant difference test).

The Bolivian tropical assemblage was the most distinctive of the four in terms of trait relationships. Only at the Bolivian site was final height associated with leaf habit, rather than with LDMC (Table 4; Figure 5B): tall trees at this site were often deciduous or semi-deciduous, whereas all trees attaining ≤ 20 m height were evergreen (Appendix 1).

Discussion

Strong convergence of trait means at temperate rainforest sites

Our comparison of trait means showed strong evidence of trait convergence at the temperate forest sites (Table 3): trait centroids of assemblages at climatically matched temperate sites in Chile and New Zealand were not significantly different, and were much closer to each other than to those of either of the non-temperate assemblages (Figure 2). This presumably reflects environmental filtering of the traits we included, or of other related traits, and is consistent with global but less detailed studies showing strong and consistent

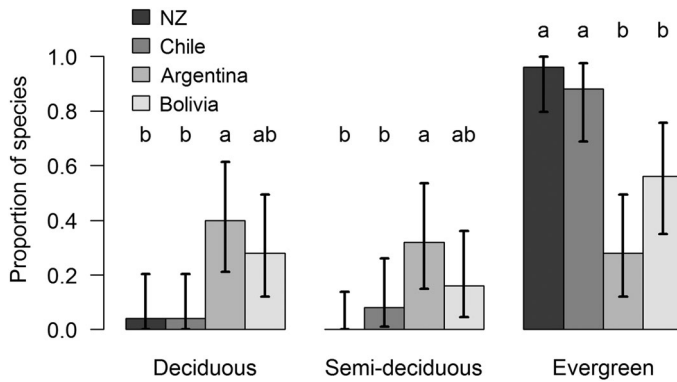


Figure 4. Distribution leaf habit in tree assemblages of four humid forests: two temperate (New Zealand, Chile), one subtropical (Argentina) and one tropical (Bolivia). Sites sharing the same letter do not differ significantly at $P = 0.05$. Error bars show 95% confidence intervals.

Table 4. Summary of principal component analyses of each tree assemblage, showing percentages of variance explained by the first two axes, and trait loadings on axes as measured by Kendall's tau.

Trait	Site							
	New Zealand		Chile		Argentina		Bolivia	
	Axis 1 (43.1%)	Axis 2 (19.6%)	Axis 1 (31.4%)	Axis 2 (22.3%)	Axis 1 (50.6%)	Axis 2 (16.8%)	Axis 1 32.3%	Axis 2 23.6%
Final height	-0.552	-0.064	-0.767	-0.280	-0.391	0.230	0.257	0.527
Twig wood density	-0.584	-0.364	-0.373	0.313	-0.745	-0.130	-0.637	-0.037
Leaf habit	-0.024	0.189	-0.056	-0.378	-0.105	-0.772	-0.205	-0.693
Leaf dry matter content	-0.682	-0.254	-0.555	-0.154	-0.727	-0.027	-0.691	0.050
(log) Leaf size	0.491	-0.184	-0.090	-0.626	0.598	-0.017	-0.074	0.328
(log) Seed mass	-0.497	-0.304	-0.281	-0.140	-0.533	0.007	-0.553	0.173
Pollination syndrome	0.327	-0.625	0.469	-0.341	-0.462	-0.300	-0.156	0.099

Bold = $P \leq 0.05$; bold and underlined = $P \leq 0.01$.

trends in trait means along major environmental gradients (e.g. Swenson & Enquist 2007; Freschet et al. 2011; Swenson et al. 2012).

Some of the patterns revealed by our comparisons (Figures 3, 4) are well-documented, in particular the latitudinal trends in leaf and seed sizes in humid forests (Webb 1968; Lord et al. 1997; Kooyman et al. 2012). Although neither of these trends is well-understood, optimization of water use efficiency provides one possible basis for explaining geographic variation in leaf size (Parkhurst & Loucks 1972). Small leaves may also be advantageous in

Table 5. Pearson correlations between principal component analysis axis trait loadings of different tree assemblages, summarizing similarities of trait relationships across the four sites.

	New Zealand	Chile	Argentina	Bolivia
New Zealand		-0.24	-0.31	-0.41
Chile	0.81		0.19	-0.03
Argentina	0.78	0.30		0.94
Bolivia	0.45	0.17	0.54	

Correlations of trait loadings on principal component analysis axis 1 are shown to the lower left of the diagonal, and those for axis 2 are shown on the upper right. A strong positive correlation indicates that the relevant pair of assemblages shares similar trait relationships. Bold = $P \leq 0.05$; bold and underlined = $P \leq 0.01$.

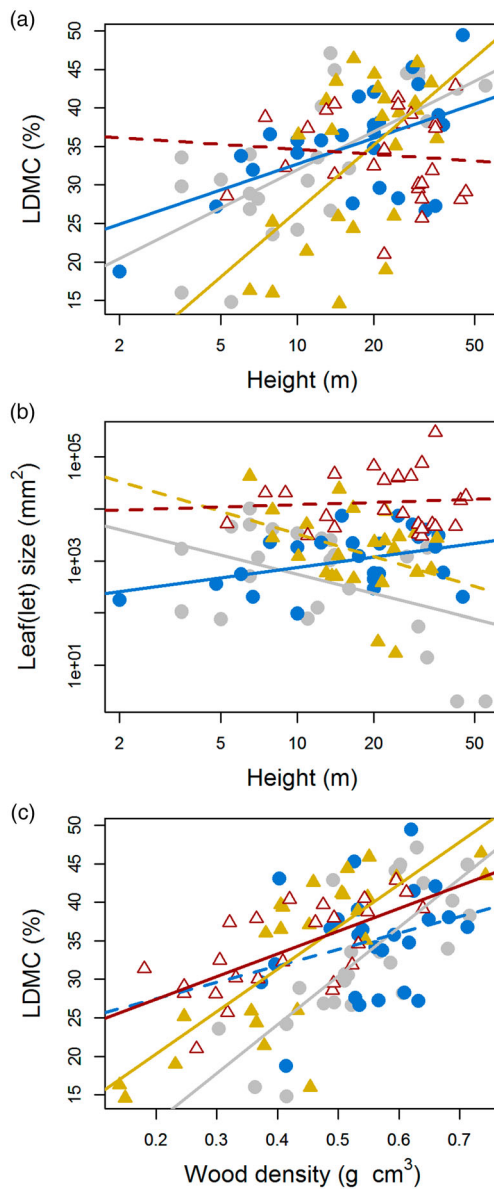


Figure 5. Bivariate trait relationships of humid forest tree assemblages. Grey dots = New Zealand temperate species; blue dots = Chilean temperate species; gold triangles = Argentine subtropical species; red triangles = Bolivian tropical species. Solid lines show ordinary least squares relationships significant at $P \leq 0.05$, dashed lines show non-significant relationships. Correlation matrices for bivariate relationships are given in Appendix 1.

some temperate environments because their thin boundary layers keep them close to air temperatures, reducing the risk of frost damage through strong radiative cooling on clear nights (Leuning & Cremer 1988). In contrast, the greater incidence of deciduousness at the Bolivian and Argentine sites cannot be generalized as typical of temperate versus (sub)tropical comparisons, as tropical rainforests on sites with less seasonal rainfall patterns are overwhelmingly dominated by evergreens (e.g. Reich et al. 1991).

On the other hand, our finding of higher mean wood density at the temperate sites than at their (sub)tropical counterparts is an apparent departure from other published results. A global study by Swenson and Enquist (2007) reported a negative correlation of wood density with latitude, and a positive correlation with mean annual temperature. We note, however, that their study includes all woody biomes, not just humid forests, and that their positive correlation with latitude all but disappeared when phylogeny was taken into account. However, like us, Swenson and Enquist (2007) found a narrower range of wood densities in the temperate zone, suggesting stronger environmental filtering of wood traits in mid-latitude forests than in the tropics (Swenson & Enquist 2007). Our tropical and subtropical assemblages included species with very low wood densities ($< 0.3 \text{ g cm}^{-3}$) that are mostly fast-growing, light-demanding trees that regenerate in tree-fall gaps (Easdale & Healey 2009; Poorter et al. 2010), a functional group usually absent from mid-latitude rainforests (Lusk et al. 2011). Differences in methodology might have also influenced our wood density data, as bark and phloem were stripped from twigs before measurement of wood volume and dry weight in New Zealand, Chile and Argentina, but not in tropical Bolivia.

Partial convergence of trait associations at temperate rainforest sites

We also found significant convergence of trait relationships in the two temperate assemblages, in that trait loadings on the first PCA axis were similar (Table 5). In both the Chilean and New Zealand assemblages, the major axis of variation was dominated by a strong positive relationship between final height and LDMC (Table 4; Figure 5B). The principal axis of functional variation in both temperate assemblages thus extends from small short-lived trees with soft leaves that occupy forest understories and tree-fall gaps (low scores on PCA axis 1 in Figure 2), to long-lived emergent trees with sclerophyllous leaves (the highest scores on PCA axis 1). Moderately long-lived canopy trees have moderate to high scores on axis 1 e.g. Myrtaceae in Chile, Atherospermataceae in both regions. Although a similar association of height with LDMC was also present in Argentina (Table 5), the subtropical assemblage lacked any close analogues of the emergent trees found at the two temperate sites: podocarps in New Zealand and Chilean *Nothofagus* spp. share a combination of tall stature ($\geq 35 \text{ m}$), small, sclerophyllous leaves and relatively dense wood. Most other emergent trees in the temperate rainforests of the southern hemisphere (including those of southeastern Australia that are not represented here) are either evergreen conifers (Enright & Hill 1995) or evergreen species of *Nothofagus* with leaves of similar constitution to those of *Nothofagus dombeyi* (Veblen et al. 1996a), confirming that small, sclerophyllous leaves are a generalized feature of emergent trees in this biome. Regeneration of most emergent trees in temperate rainforests is associated with coarse-scale disturbances, at least on sites where there is vigorous competition from broad-leaved trees and shrubs (Enright & Hill 1995; Veblen et al. 1996a; Veblen et al. 2016). Although tall *Eucalyptus* species such as *Eucalyptus obliqua* and *Eucalyptus regnans* also occur as emergents in early- to mid-successional rainforest stands in southeastern Australia, they differ from typical rainforest emergent trees in their fire-dependence and their attainment of great size through rapid growth rather than great longevity (Tng et al. 2012).

Apart from emergent trees, small trees with small leaves and fairly dense twigs represent another trait combination confined to the two temperate sites (Figure 5). These

species score low on axis 2 of the combined PCA (Figure 2). Most such species in the New Zealand assemblage are divaricate shrubs such *Melicytus micranthus* and *Coprosma areolata*, or trees with a divaricate juvenile phase such as *Pennantia corymbosa* (Kelly 1994). Although we are not aware of any Chilean rainforest species with divaricate branching, a few small trees such as *Azara lanceolata* and *Lomatia ferruginea* share the characteristics of small leaves or leaflets ($< 6 \text{ cm}^2$) and fairly dense wood ($> 0.5 \text{ g cm}^3$).

A notable difference between the two temperate assemblages was the much higher representation of small trees with large, soft leaves in New Zealand (Figure 5B,C). McGlone et al. (2010) showed that New Zealand in general is richer in small trees than most other temperate regions, which they attributed to allopatric speciation, radiation and differential extinction resulting from the geomorphic dynamism of the New Zealand archipelago during the late Neogene, and from cyclic contraction and fragmentation of forest vegetation during glacial periods. These dynamics might have favoured small trees with short generation times that were able to maintain viable populations in small areas of forest, and discriminated against larger, slower-maturing trees with lower population densities (McGlone et al. 2010). Another factor that might have contributed to the lower richness of small trees in the Chilean assemblage is competition from the *Chusquea* bamboos that pervade lowland forest understoreys in temperate South America. *Chusquea* spp. form thickets up to 10 m tall in tree-fall gaps (Veblen et al. 1996b; González et al. 2002), reducing light to levels similar to those found under tall closed-canopy forest (Lusk 2001). Although tree ferns proliferate in tree-fall gaps in New Zealand lowland forests (Beveridge 1973), their relatively slow growth often allows small, fast-growing trees and shrubs to complete their life cycles during the window of opportunity afforded by these fine-scale disturbances (Ogden et al. 1991; Wardle 1991). Since the diversification of *Chusquea* in South American temperate forests, probably later than the mid-Miocene (Villagrán & Hinojosa 1997; Fisher et al. 2014), tree-fall gaps there would have become a less hospitable environment for small trees to survive to maturity, and hence specialize in evolutionary time; this may help to explain the paucity of trees $< 10 \text{ m}$ tall in the Chilean assemblage (Figure 5). Additionally, the prevalence of soft leaves among most small trees in the New Zealand assemblage might reflect the historical absence of browsing mammals there. Uncontrolled populations of introduced mammals often deplete soft-leaved taxa such as *Coprosma* spp., *Pseudopanax* spp., *Schefflera digitata* and *Melicytus* spp. in New Zealand forests (Forsyth et al. 2002), and the leaf traits of the contemporary Chilean assemblage will, to some degree, reflect historical filtering by interaction with the mammalian herbivores that have been present in South America throughout the Cenozoic (Flynn & Wyss 1998; Woodburne et al. 2014). The historical influence of avian herbivores on the evolution of New Zealand plants remains a matter of contention (Lee et al. 2010; McGlone et al. 2010).

Imperfect matching of regional climates is another potential cause of functional differences between the two temperate assemblages. Despite considerable overlap in the climatic variables that we chose to compare (summer rainfall, summer maximum temperatures and winter minimum temperatures), the two regions differ on average in seasonality of rainfall, with Chilean and Argentine sites on average receiving a much larger fraction of their annual precipitation during winter (Appendix 1). Although we did not gather data on inter-annual variation in rainfall, this factor has been invoked to explain functional differences between plant assemblages of different Mediterranean regions (Cowling et al. 2005).

It is pertinent to ask how well the organ-level traits we measured represent species performance, life history dimensions and environmental tolerances (Easdale & Healey 2009; Craine et al. 2012). A trade-off between juvenile growth rate and shade tolerance appears to represent a major axis of life history variation in tropical rainforest assemblages, and species positions on this trade-off have been linked to wood density and leaf economic traits (Sterck et al. 2006; Wright et al. 2010). In temperate rainforests, species differences in longevity and population turnover rates may be just as important as growth versus shade tolerance trade-offs in shaping forest structure and dynamics (Ogden & Stewart 1995; Chesson 2000; Lusk et al. 2015). Commensurable data on juvenile growth rates and shade tolerance are available for few of the species in our two temperate assemblages, but species scores on PCA axis one (Figure 2) seem more closely related to longevity and population turnover rates than to shade tolerance or successional status (Tortorelli 1956; Wardle 1991; Ogden & Stewart 1995; Gutiérrez & Huth 2012). Although species differences in shade tolerance are undoubtedly also influential in temperate rainforests, species scores on the first two PCA axes do not appear to relate closely to shade tolerance, underlining the difficulty of using organ-level traits to index this elusive life history dimension (Craine et al. 2012).

Conclusions

As far as we are aware, this is the first study to statistically test whether disjunct tree assemblages on climatically and topographically matched sites are more functionally similar to each other than to assemblages from other environments. Our analysis showed close convergence of mean trait values at temperate forest sites in Chile and New Zealand, and partial convergence in trait combinations. Several differences between the respective biogeographic histories of New Zealand and southern South America could have influenced current divergences in trait combinations, in particular the greater abundance of small trees with large soft leaves in New Zealand. Testing historical hypotheses is problematic, and inference of extinction events from molecular phylogenies remains controversial (Bokma 2008; Rabosky & Lovette 2008; Rabosky 2010), but important insights into the evolutionary history of lineages have been gained by complementing the fossil record with molecular phylogenies (e.g. Schneider et al. 2004; Biffin et al. 2012). These successes give grounds for hoping that functional differences between the disjunct rainforest assemblages of the southern hemisphere may eventually be better understood.

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Appendix 1

Table A1. Descriptors of climate at selected temperate forest sites in New Zealand and temperate South America. Asterisks show variables used for climatic matching of sites.

Site	Latitude (°)	Longitude (°)	Mean annual temp. (°C)	Diurnal range (°C)	Mean daily maximum of warmest month (°C)*	Mean daily minimum of coldest month (°C)*	Mean annual precip. (mm)	Rainfall of warmest quarter (mm)*
<i>(a) New Zealand</i>								
Manukau Heads	-37.04	174.57	14.6	6	22.5	8.1	1124	234
Pukekohe	-37.20	174.89	14.5	8.3	23.7	6.4	1283	212
Mt. Te Aroha	-37.53	175.74	8.5	6.2	17	1.7	2094	397
Tauranga	-37.70	176.16	14.8	9.3	24	5.9	1181	253
Hamilton	-37.87	175.33	13.8	10.2	24.3	4	1108	224
Whakatane	-37.95	176.99	14.3	10.2	24.1	4.1	1535	353
Opotiki	-38.01	177.28	13.9	9.6	23.1	4.4	1409	323
Rotorua	-38.11	176.32	12.7	9.2	22.9	3.5	1342	301
Pureora	-38.52	175.55	10.6	9.6	21.2	1.3	1710	332
Gisborne	-38.66	177.98	14.5	10.4	24.9	4.6	1050	186
Taupo	-38.74	176.08	11.7	10.2	22.7	2.1	960	239
Waikaremoana	-38.80	177.12	11.4	8.2	21.4	3.2	2088	489
Taumaranui	-38.88	175.26	12.8	11	24.3	2.4	1522	339
Turangi	-38.99	175.81	11.9	10.3	23	1.7	1616	350
New Plymouth	-39.01	174.18	13.7	7.5	22.1	5.8	1398	326
Wairoa	-39.03	177.42	14.2	10	24	4.8	1308	281
Whakapapa	-39.20	175.54	7.5	9	17.9	-0.6	2759	530
Stratford	-39.34	174.28	11.8	8.6	21.2	3.8	2022	394
Ohakune Junction	-39.40	175.41	10	9.3	20.8	0.4	1418	282
Hastings	-39.64	176.84	14.4	11	25.5	3.6	724	172
Taihape	-39.68	175.80	11.4	9	22.2	2.8	920	211
Patea	-39.75	174.47	13.5	6.9	21.2	5.7	1048	218
Wanganui	-39.93	175.05	14.1	7.8	22.7	5.6	917	198
Waipukurau	-40.00	176.56	12.7	10.7	24.3	3	835	187
Marton	-40.07	175.38	12.1	8.7	21.9	3.4	1017	217
Dannevirke	-40.21	176.10	12.4	9	22.6	3.6	1057	224
Palmerston North	-40.32	175.62	13.1	9.3	23.5	4.6	918	175
Levin	-40.62	175.28	13.1	8.4	22.4	4.3	1082	216
Mt Bruce	-40.72	175.64	11.6	9.4	22	2.8	2111	452
Paraparaumu	-40.90	174.98	13	7.5	21.4	4.7	976	176
Masterton	-40.95	175.65	12.8	10.6	24.3	3.1	923	184
Gladstone	-41.08	175.65	12.2	10.5	23	2.4	936	169
Motueka	-41.12	173.01	12.5	11.1	23.2	1.4	1418	262
Pelorus Sound	-41.17	173.90	13.6	7.3	22	5.8	1747	353
Wairongomai	-41.26	175.15	12.8	8	21.8	5	1475	294
Nelson	-41.30	173.22	12.7	9.6	22.6	1.9	960	244
Wellington	-41.33	174.81	12.9	6	20.6	6.3	1207	233
Blenheim	-41.51	173.87	12.6	11.6	24.1	1.5	711	156
Westport	-41.74	171.58	12.6	7.5	20.6	4.6	2274	493
Murchison	-41.80	172.33	11.4	11.1	24	0.9	1527	305
St Arnaud	-41.80	172.85	9.2	11.1	21.1	-1.5	1548	390
Molesworth	-42.09	173.26	8.2	12.5	21.3	-3.3	630	147
Reefton	-42.12	171.86	11.4	10.6	23.1	0.5	1943	441
Kaikoura	-42.41	173.68	12.4	6.7	20.6	5.1	844	198
Greymouth	-42.46	171.19	12.2	8.1	20.5	3.2	2479	542
Hokitika	-42.71	170.98	11.7	8	19.9	2.9	2901	653
Waipara	-43.06	172.75	12	9.1	23.6	1.2	619	152
Rangiora	-43.30	172.59	11.4	11.1	22.4	0.7	664	153

(Continued)

Table A1. Continued.

Site	Latitude (°)	Longitude (°)	Mean annual temp. (°C)	Diurnal range (°C)	Mean daily maximum of warmest month (°C)*	Mean daily minimum of coldest month (°C)*	Mean annual precip. (mm)	Rainfall of warmest quarter (mm)*
Fox Glacier	-43.46	170.02	10.9	9.2	20.1	1.8	4624	1178
Christchurch	-43.49	172.54	12.2	9.9	22.7	1.9	618	130
Akaroa	-43.80	172.97	12.5	10	23	2.9	969	166
Chatham Ids	-43.82	-176.47	11.5	5.1	18.2	5.9	911	204
Haast	-43.88	169.05	11.2	7.6	18.6	3.5	3355	893
Ashburton	-43.91	171.74	11.7	11.4	23.7	0.5	696	168
Peel Forest	-43.92	171.26	10.3	12.2	21.4	-1.1	1066	326
Tekapo	-44.01	170.50	8.7	11.1	21.6	-3	591	132
Geraldine	-44.09	171.24	11	11.4	22.5	-0.3	796	232
Timaru	-44.30	171.23	10.6	11.3	21.5	-0.6	547	151
Wanaka	-44.70	169.13	10.7	12.1	23.9	-1.2	673	159
Oamaru	-44.97	171.08	10.5	9.4	19.8	0.8	473	134
Queenstown	-45.02	168.74	9.7	10.6	21.8	-1.7	749	168
Alexandra	-45.24	169.38	11	13.4	25.1	-2.4	359	112
Palmerston	-45.48	170.71	10.2	11	20.3	-0.2	648	168
Manapouri	-45.57	167.62	9.3	10.7	20.8	-0.7	1129	275
Dunedin	-45.93	170.20	11.1	7	18.9	3.1	738	228
Gore	-46.10	168.95	9.8	8.8	19.3	1	955	281
Milton	-46.12	169.96	8.6	12.3	21.4	-2.7	593	211
Tuatapere	-46.14	167.69	10.5	10	19.8	1.5	1238	390
Balclutha	-46.24	169.74	10.4	9.6	20.1	1.7	685	198
Invercargill	-46.42	168.32	10	8.9	18.7	1	1149	307
Stewart Island	-46.99	167.83	9.9	7.3	17.3	2.6	1590	386
<i>(b) South America</i>								
Concepción	-36.82	-73.04	12.8	9.1	22.1	5.9	1131	55
Isla Santa Maria	-37.02	-73.52	12.2	5.7	18.3	7.3	876	63
Punta Lavapie	-37.15	-73.58	13.3	6.7	20.4	7.2	804	56
Lebu	-37.61	-73.65	13	7.8	22.4	6.7	1302	114
Angol	-37.81	-72.70	12.8	12.2	27	4.1	953	54
Contulmo	-38.01	-73.23	12.6	12.5	26.1	4.8	1896	143
Victoria	-38.23	-72.35	12.4	11.9	26.1	2.1	1329	141
Traiguén	-38.25	-72.68	12	11.9	26.8	3.8	1241	101
Isla Mocha	-38.35	-73.93	12.6	5.8	18.2	6.9	1373	136
Cullinco	-38.36	-72.27	10.6	11.2	24.8	2.3	1558	133
Lonquimay	-38.45	-71.37	8.6	15.5	25.4	-2.6	1995	164
Temuco	-38.73	-72.60	11.8	10.8	23.4	4	1212	128
Puerto Dominguez	-38.90	-73.25	11.5	9.4	20.4	4.5	1581	137
Valdivia airport	-39.80	-73.24	12.9	9.3	22.9	4.5	1788	160
Punta Galera	-40.01	-73.71	11.3	5.3	16.5	6.4	2077	214
Rio Bueno	-40.33	-72.95	11.3	11.1	23.7	3.4	1235	139
Osorno	-40.57	-73.12	12.6	9	22	4.2	1319	159
Aguas Calientes	-40.74	-72.31	8.9	10.7	20.4	0.8	3593	567
Frutillar	-41.12	-73.05	10.3	9	20	3.1	1659	236
Bariloche	-41.15	-71.36	8.1	11.8	21.4	-1.3	783	72
Puerto Montt	-41.47	-72.94	10.3	8.2	19.2	3.5	1765	267
Mauillin	-41.62	-73.60	9.7	9	19.9	3.4	1915	287
Ancud	-41.87	-73.83	11.1	5.7	17.8	5.2	2540	361
El Bolson	-41.97	-71.54	9.7	13.5	24.1	-0.5	923	98
Castro	-42.48	-73.76	11.6	11	20.4	2.1	1599	200
Esquel	-42.91	-71.32	8.2	12	21	-2.9	504	61
Chaitén	-42.92	-42.92	11.2	6.1	17.8	4.9	3619	631
Quellon	-43.12	-73.61	11.3	5.2	17.8	5.4	1961	321
Futuleufu	-43.18	-71.87	10.6	8.4	20.8	1	2081	275

(Continued)

Table A1. Continued.

Site	Latitude (°)	Longitude (°)	Mean annual temp. (°C)	Diurnal range (°C)	Mean daily maximum of warmest month (°C)*	Mean daily minimum of coldest month (°C)*	Mean annual precip. (mm)	Rainfall of warmest quarter (mm)*
Melinka	-43.90	-73.75	10	6.4	17.4	4.6	3138	537
Rio Cisnes	-44.55	-71.38	7.6	11.9	19.1	-4.7	702	96
Puerto Aysén	-45.40	-72.69	9	7.1	17.9	1.7	2941	502
Coyhaique	-45.57	-72.08	9.5	7.6	18.5	0.2	994	162
Balmaceda	-45.92	-71.69	7.3	10.5	19.4	-3.8	572	105
Cabo Raper	-46.80	-75.64	8.6	5.6	14.2	3.7	1950	462

Table A2. Mean trait values of 25 common tree species from each of four humid forest assemblages, from two climatically matched temperate sites (in New Zealand and Chile), plus a subtropical site (Argentina) and a tropical site (Bolivia).

Species	Family	Code	Height (m)	Wood density (g cm ⁻³)	Leaf habit	LDMC (%)	Leaf size (mm ²)	Seed mass (mg)	Pollination syndrome
<i>(a) Palmerston North, New Zealand</i>									
<i>Meliclytus micranthus</i>	Violaceae	MELMIC	3.5	0.568	Evergreen	33.6	108	3.5	Biotic
<i>Melicope simplex</i>	Rutaceae	MELSIM	3.5	0.510	Evergreen	29.8	106	5.9	Biotic
<i>Geniostoma rupestre</i>	Loganiaceae	GENRUP	3.5	0.363	Evergreen	16.0	1733	0.30	Biotic
<i>Coprosma areolata</i>	Rubiaceae	COPARE	5.0	0.511	Evergreen	30.7	76	5.6	Wind
<i>Piper excelsum</i>	Piperaceae	PIPEXC	5.5	0.415	Evergreen	14.8	4597	1.9	Wind
<i>Myrsine australis</i>	Myrsinaceae	MYRAUS	6.5	0.680	Evergreen	34.0	516	17	Wind
<i>Coprosma grandifolia</i>	Rubiaceae	COPGRA	6.5	0.476	Evergreen	26.9	5060	23	Wind
<i>Brachyglottis repanda</i>	Asteraceae	BRAREP	6.5	0.436	Evergreen	28.9	10180	0.05	Biotic
<i>Hoheria sexstylosa</i>	Malvaceae	HOHSEX	7.0	0.606	Evergreen	28.2	1159	6.1	Biotic
<i>Schefflera digitata</i>	Araliaceae	SCHDIG	8.0	0.303	Evergreen	23.6	4118	0.6	Biotic
<i>Meliclytus ramiflorus</i>	Violaceae	MELRAM	10.0	0.415	Evergreen	24.2	3382	1.1	Biotic
<i>Pennantia corymbosa</i>	Pennantiaceae	PENCOR	11.0	0.516	Evergreen	30.6	79	17	Biotic
<i>Streblus heterophyllus</i>	Moraceae	STRHET	12.0	0.521	Evergreen	33.6	126	19	Wind
<i>Pittosporum eugenioides</i>	Pittosporaceae	PITEUG	12.5	0.688	Evergreen	40.2	2705	7.4	Biotic
<i>Alectryon excelsus</i>	Sapindaceae	ALEEXC	13.5	0.629	Evergreen	47.1	1045	205	Biotic
<i>Hedycarya arborea</i>	Monimiaceae	HEDARB	13.5	0.522	Evergreen	26.7	2536	170	Biotic
<i>Nestegis lanceolata</i>	Oleaceae	NESLAN	14.0	0.712	Evergreen	44.9	1302	35	Biotic
<i>Plagianthus regius</i>	Malvaceae	PLAREG	16.0	0.586	Deciduous	32.2	296	4.2	Biotic
<i>Beilschmiedia tawa</i>	Lauraceae	BEITAW	27.0	0.600	Evergreen	44.5	1214	1375	Biotic
<i>Podocarpus totara</i>	Podocarpaceae	PODTOT	30.0	0.594	Evergreen	44.1	56	16	Wind
<i>Knightsia excelsa</i>	Proteaceae	KNIEXC	30.0	0.602	Evergreen	44.9	3252	24	Biotic
<i>Prumnopitys taxifolia</i>	Podocarpaceae	PRUTAX	32.5	0.716	Evergreen	38.3	14	106	Wind
<i>Laurelia novaezelandiae</i>	Atherospermataceae	LAUNOV	32.5	0.493	Evergreen	27.0	1793	11	Biotic
<i>Dacrydium cupressinum</i>	Podocarpaceae	DACCUP	42.5	0.640	Evergreen	42.5	2	4.8	Wind
<i>Dacrycarpus dacrydioides</i>	Podocarpaceae	DACDAC	55.0	0.491	Evergreen	42.9	2	10.0	Wind
<i>(b) Valdivia, Chile</i>									
<i>Fuchsia magellanica</i>	Onagraceae	FUCMAG	2.0	0.414	Semi-dec.	18.8	177	0.40	Biotic
<i>Azara lanceolata</i>	Flacourtiaceae	AZALAN	4.8	0.632	Evergreen	27.2	363	2.7	Biotic
<i>Raukawa laetevirens</i>	Araliaceae	RAULAE	6.0	0.572	Evergreen	33.8	560	3.5	Biotic
<i>Rhaphithamnus spinosus</i>	Verbenaceae	RHASPI	6.7	0.396	Evergreen	32.0	206	31	Biotic
<i>Aristotelia chilensis</i>	Elaeocarpaceae	ARICHI	7.8	0.487	Evergreen	36.6	2326	12	Biotic
<i>Lomatia dentata</i>	Proteaceae	LOMDEN	10.0	0.561	Evergreen	34.2	1829	7.4	Biotic
<i>Lomatia ferruginea</i>	Proteaceae	LOMFER	10.0	0.533	Evergreen	35.8	99	7.8	Biotic

(Continued)

Table A2. Continued.

Species	Family	Code	Height (m)	Wood density (g cm ⁻³)	Leaf habit	LDMC (%)	Leaf size (mm ²)	Seed mass (mg)	Pollination syndrome
<i>Myrceugenia planipes</i>	Myrtaceae	MYRPLA	12.4	0.592	Evergreen	35.8	2271	46	Biotic
<i>Lomatia hirsuta</i>	Proteaceae	LOMHIR	15.0	0.540	Evergreen	36.5	7435	4.7	Biotic
<i>Embothrium coccineum</i>	Proteaceae	EMBIOC	16.5	0.528	Semi-dec.	27.6	2223	14	Biotic
<i>Blepharocalyx cruckshanksii</i>	Myrtaceae	BLECRU	17.5	0.624	Evergreen	41.5	1252	14	Biotic
<i>Amomyrtus luma</i>	Myrtaceae	AMOLUM	20.0	0.660	Evergreen	42.1	582	29	Biotic
<i>Amomyrtus meli</i>	Myrtaceae	AMOMEL	20.0	0.712	Evergreen	36.8	448	31	Biotic
<i>Maytenus boaria</i>	Celastraceae	MAYBOA	20.0	0.616	Evergreen	34.8	295	16	Biotic
<i>Luma apiculata</i>	Myrtaceae	LUMAPI	20.0	0.499	Evergreen	37.8	460	17	Biotic
<i>Podocarpus salignus</i>	Podocarpaceae	PODSAL	21.0	0.682	Evergreen	38.1	574	45	Wind
<i>Gevuina avellana</i>	Proteaceae	GEVAVE	21.1	0.373	Evergreen	27.5	2151	1495	Biotic
<i>Drimys winteri</i>	Winteraceae	DRIWIN	25.0	0.609	Evergreen	28.3	7437	4.7	Biotic
<i>Aextoxicon punctatum</i>	Aextoxiceae	AEXPUN	28.5	0.526	Evergreen	45.3	5060	350	Biotic
<i>Persea lingue</i>	Lauraceae	PERLIN	30.0	0.403	Evergreen	43.1	2930	690	Biotic
<i>Laureliopsis philippiana</i>	Atherospermataceae	LAUPHI	32.0	0.535	Evergreen	26.7	4050	1.6	Biotic
<i>Laurelia sempervirens</i>	Atherospermataceae	LAUSEM	35.0	0.566	Evergreen	27.3	1895	3.3	Biotic
<i>Eucryphia cordifolia</i>	Cunoniaceae	EUCCOR	36.0	0.532	Evergreen	39.1	3126	1.7	Biotic
<i>Nothofagus obliqua</i>	Nothofagaceae	NOTOBL	37.5	0.649	Deciduous	37.8	599	124	Wind
<i>Nothofagus dombeyi</i>	Nothofagaceae	NOTDOM	44.7	0.620	Evergreen	49.5	206	1.8	Wind
(c) Sierra de San Javier, Tucumán, Argentina									
<i>Urera baccifera</i>	Urticaceae	UREBAC	6.5	0.140	Deciduous	16.3	43135	2.2	Wind
<i>Boehmeria caudata</i>	Urticaceae	BOECAU	8.0	0.246	Semi-dec.	25.2	9576	0.05	Wind
<i>Vassobia breviflora</i>	Solanaceae	VASBRE	8.0	0.454	Semi-dec.	16.0	2780	0.36	Biotic
<i>Duranta serratifolia</i>	Verbenaceae	DURSER	10.1	0.405	Deciduous	36.5	1225	25	Biotic
<i>Piper tucumanum</i>	Piperaceae	PIPTUC	10.9	0.378	Evergreen	21.4	5094	2.4	Biotic
<i>Allophylus edulis</i>	Sapindaceae	ALLEDU	13.0	0.508	Semi-dec.	41.0	591	37	Biotic
<i>Chrysophyllum marginatum</i>	Sapotaceae	CHRMAR	13.7	0.452	Evergreen	37.1	513	44	Biotic
<i>Eugenia uniflora</i>	Myrtaceae	EUGUNI	14.2	0.742	Semi-dec.	43.5	502	100	Biotic
<i>Tecoma stans</i>	Bignoniaceae	TECSTA	14.5	0.357	Semi-dec.	25.9	1269	4.6	Biotic
<i>Urera caracasana</i>	Urticaceae	URECAR	14.6	0.149	Deciduous	14.6	24321	0.24	Wind
<i>Solanum riparium</i>	Solanaceae	SOLRIP	16.6	0.365	Evergreen	24.4	10453	0.77	Biotic
<i>Eugenia pungens</i>	Myrtaceae	EUGPUN	16.7	0.735	Evergreen	46.4	457	210	Biotic
<i>Tabebuia impetiginosa</i>	Bignoniaceae	TABIMP	20.1	0.515	Deciduous	44.4	2295	77	Biotic
<i>Jacaranda mimosifolia</i>	Bignoniaceae	JACMIM	20.8	0.459	Deciduous	42.6	28	9.3	Biotic
<i>Terminalia triflora</i>	Combretaceae	TERTRI	21.6	0.532	Deciduous	38.9	387	10	Biotic
<i>Cupania vernalis</i>	Sapindaceae	CUPVER	22.1	0.506	Evergreen	41.2	2473	364	Biotic
<i>Heliocarpus popayanensis</i>	Malvaceae	HELPOP	22.3	0.232	Deciduous	19.0	9063	1.7	Biotic

(Continued)

Table A2. Continued.

Species	Family	Code	Height (m)	Wood density (g cm ⁻³)	Leaf habit	LDMC (%)	Leaf size (mm ²)	Seed mass (mg)	Pollination syndrome
<i>Myrsine laetevirens</i>	Myrsinaceae	MYRLAE	24.0	0.433	Evergreen	26.0	1706	17	Wind
<i>Parapiptadenia excelsa</i>	Fabaceae	PAREXC	24.4	0.545	Deciduous	35.1	17	20	Biotic
<i>Juglans australis</i>	Juglandaceae	JUGAUS	25.2	0.409	Deciduous	39.4	2947	6353	Wind
<i>Cinnamomum porphyrium</i>	Lauraceae	CINPOR	29.1	0.548	Evergreen	40.7	3488	456	Biotic
<i>Tipuana tipu</i>	Fabaceae	TIPTIP	29.5	0.405	Deciduous	39.7	613	564	Biotic
<i>Ruprechtia laxiflora</i>	Polygonaceae	RUPLAX	29.7	0.551	Semi-dec.	45.9	608	9.1	Biotic
<i>Blepharocalyx salicifolius</i>	Myrtaceae	BLESAL	33.7	0.596	Semi-dec.	43.3	705	29	Biotic
<i>Cedrela lilloi</i>	Meliaceae	CEDLIL	35.4	0.381	Semi-dec.	36.0	2743	19	Biotic
(d) La Chonta, Bolivia									
<i>Erythrochiton fallax</i>	Rutaceae	ERYFAL	5.3	0.490	Evergreen	28.6	5260	64	Biotic
<i>Picramnia sellowii</i>	Simaroubaceae	PICSEL	7.5	0.548	Evergreen	38.8	20400	53	Biotic
<i>Guarea guidonea</i>	Meliaceae	GUAGUI	9.0	0.409	Evergreen	32.3	20476	107	Biotic
<i>Hirtella triandra</i>	Chrysobalanaceae	HIRTRI	11.0	0.462	Evergreen	37.4	3094	104	Biotic
<i>Alibertia verrucosa</i>	Rubiaceae	ALIVER	13.0	0.475	Evergreen	39.7	7200	40	Biotic
<i>Licaria triandra</i>	Lauraceae	LICTRI	14.0	0.543	Evergreen	40.5	4375	1237	Biotic
<i>Triplaris americana</i>	Polygonaceae	TRIAME	14.0	0.181	Evergreen	31.4	47410	25	Biotic
<i>Pourouma cecropiifolia</i>	Urticaceae	POUCEC	20.0	0.305	Evergreen	32.5	67486	297	Wind
<i>Heliocarpus americanus</i>	Malvaceae	HELAME	22.0	0.267	Semi-dec.	21.0	9417	1.5	Biotic
<i>Sapindus saponaria</i>	Sapindaceae	SAPSAP	22.0	0.533	Deciduous	34.6	35926	1052	Biotic
<i>Inga edulis</i>	Fabaceae	INGEDU	25.0	0.612	Evergreen	41.3	39703	168	Biotic
<i>Swietenia macrophylla</i>	Meliaceae	SWIMAC	25.0	0.420	Deciduous	40.4	41835	407	Biotic
<i>Batocarpus amazonicus</i>	Moraceae	BATAMA	26.0	0.365	Evergreen	37.9	8190	213	Wind
<i>Aspidosperma rigidum</i>	Apocynaceae	ASPRIG	30.0	0.492	Deciduous	29.5	3297	151	Biotic
<i>Ormosia nobilis</i>	Fabaceae	ORMNOB	28.0	0.639	Evergreen	39.2	42995	479	Biotic
<i>Maclura tinctoria</i>	Moraceae	MACTIN	30.0	0.368	Semi-dec.	30.1	5144	2.8	Wind
<i>Sapium glandulosum</i>	Euphorbiaceae	SAPGLA	31.0	0.246	Evergreen	28.2	3013	7.8	Biotic
<i>Trema micrantha</i>	Ulmaceae	TREMIC	31.0	0.318	Evergreen	25.7	4165	3.0	Biotic
<i>Zanthoxylum sprucei</i>	Rutaceae	ZANSPR	31.0	0.331	Deciduous	30.2	76186	22	Biotic
<i>Terminalia oblonga</i>	Combretaceae	TEROBL	34.0	0.523	Semi-dec.	31.9	5133	23	Biotic
<i>Pouteria nemorosa</i>	Sapotaceae	POUNEM	35.0	0.493	Evergreen	38.0	4600	1661	Biotic
<i>Schizolobium parahyba</i>	Fabaceae	SCHPAR	35.0	0.321	Deciduous	37.4	299170	872	Biotic
<i>Cariniana estrellensis</i>	Lecythidaceae	CAREST	42.0	0.595	Deciduous	42.9	4634	46	Biotic
<i>Hura crepitans</i>	Euphorbiaceae	HURCRE	44.0	0.298	Deciduous	28.1	14687	717	Biotic
<i>Ficus boliviana</i>	Moraceae	FICBOL	46.0	0.246	Semi-dec.	29.1	17653	0.39	Biotic

Table A3. Pearson correlation matrix of continuous variables in four humid forest assemblages.

	(log) Height	Wood density	LDMC	(log) Leaf size	(log) Seed mass
<i>(a) Palmerston North, New Zealand</i>					
(log) Height					
Wood density	0.40				
LDMC	0.64	0.75			
(log) Leaf size	-0.42	-0.32	-0.42		
(log) Seed mass	0.47	0.61	0.59	-0.18	
<i>(b) Valdivia, Chile</i>					
(log) Height					
Wood density	0.28				
LDMC	0.52	0.31			
(log) Leaf size	0.40	-0.12	0.00		
(log) Seed mass	0.33	-0.19	0.35	0.20	
<i>(c) Sierra de San Javier, Tucumán, Argentina</i>					
(log) Height					
Wood density	0.38				
LDMC	0.56	0.79			
(log) Leaf size	-0.38	-0.66	-0.64		
(log) Seed mass	0.54	0.57	0.74	-0.37	
<i>(d) La Chonta, Bolivia</i>					
(log) Height					
Wood density	-0.19				
LDMC	-0.09	0.66			
(log) Leaf size	0.07	-0.17	0.17		
(log) Seed mass	-0.10	0.47	0.60	0.27	