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1 **Changes in co-existence mechanisms along a long-term soil chronosequence**  
2 **revealed by functional trait diversity.**

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11

12 *Running title: Functional diversity along ecological gradients*

13

## 14 **Summary**

15 **1.** Functional trait diversity can reveal mechanisms of species co-existence in plant communities. Few  
16 studies have tested whether functional diversity for foliar traits related to resource use strategy  
17 increases or decreases with declining soil phosphorus (P) in forest communities.

18 **2.** We quantified tree basal area and four foliar functional traits (i.e. nitrogen (N), phosphorus (P),  
19 thickness and tissue density) for all woody species along the *c.* 120 kyr Franz Josef soil  
20 chronosequence in cool temperate rainforest, where strong shifts occur in light and soil nutrient  
21 availability (i.e. total soil P declines from 805 to 100 mg g<sup>-1</sup>). We combined the abundance and trait  
22 data in functional diversity indices to quantify trait convergence and divergence, in an effort to  
23 determine whether mechanisms of co-existence change with soil fertility.

24 **3.** Relationships between species trait means and total soil N and P were examined using multiple  
25 regression, with and without weighting of species abundances. We used Rao's quadratic entropy to  
26 quantify functional diversity at the plot scale, then compared this with random expectation, using a null  
27 model that randomizes abundances across species within plots. Taxonomic diversity was measured  
28 using Simpson's Diversity. Relationships between functional and taxonomic diversity and total soil P  
29 were examined using jackknife linear regression.

30 **4.** Leaf N and P declined and leaf thickness and density increased monotonically with declining total  
31 soil P along the sequence; these relationships were unaffected by abundance-weighting of species in the  
32 analyses. Inclusion of total soil N did not improve predictions of trait means. All measures of diversity  
33 calculated from presence/absence data were unrelated to total soil N and P. There was no evidence for a  
34 relationship between Rao values using quantitative abundances and total soil P. However, there was a  
35 strongly positive relationship between Rao, expressed relative to random expectation, and total soil P,  
36 indicating trait convergence of dominant species as soil P declined.

37 **5. Synthesis:** Our results demonstrate that at high fertility dominant species differ in resource use  
38 strategy, but as soil fertility declines over the long-term, dominant species increasingly converge on a  
39 resource-retentive strategy. This suggests that differentiation in resource use strategy is required for co-  
40 existence at high fertility but not in low fertility ecosystems.

41 **Key-words:** Determinants of plant community diversity and structure, Environmental filtering, forest  
42 ecosystem development, limiting similarity, long-term community assembly, niche complementarity,  
43 nutrient stress, phosphorus limitation, species richness, succession

44

## 45 **Introduction**

46 Changes in functional diversity for key traits linked to plant resource use strategy (Grime 1974; Wright  
47 *et al.* 2004) along ecological gradients can reveal shifts in species co-existence mechanisms (Mason *et al.*  
48 *et al.* 2011c). Changes in forest communities along soil chronosequences are amongst the best-  
49 documented gradients in ecology (Walker *et al.* 1981; Kitayama & Mueller-Dombois 1995; Peltzer *et al.*  
50 *et al.* 2010; Walker *et al.* 2010). However, no study to date has applied functional diversity indices to  
51 examine whether species coexistence mechanisms change along soil chronosequences (Peltzer *et al.*  
52 2010). This approach would complement existing knowledge of changes in taxonomic diversity  
53 (Wardle *et al.* 2008) or functional trait and species composition (e.g. Vitousek, Turner & Kitayama  
54 1995; Richardson *et al.* 2004), thus improving our understanding of the processes driving vegetation  
55 change across soil chronosequences. Theoretical and practical advances in the quantification of  
56 functional diversity (*sensu* Mason *et al.* 2005) provide a rigorous set of methods for the quantification  
57 of trait convergence and divergence (Villegger, Mason & Mouillot 2008; Mouchet *et al.* 2010; Pavoine  
58 & Bonsall 2010). This study uses functional diversity for foliar traits to test whether species co-  
59 existence mechanisms in forest communities change along a well-characterised soil chronosequence  
60 (Walker & Syers 1976; Wardle, Walker & Bardgett 2004).

## 61 62 COMPETITION, SOIL FERTILITY AND TRAIT DIVERGENCE

63 Long-term soil chronosequences embody strong soil fertility (primarily phosphorus, P) gradients  
64 (Walker & Syers 1976; Richardson *et al.* 2004), and a concomitant shift from light to soil nutrient  
65 limitation of plant growth (e.g. Coomes & Grubb 2000). Competition for light is size-asymmetric  
66 whereas competition for nutrients is size-symmetric (Schwinning & Weiner 1998; Berntson & Wayne  
67 2000; Cahill & Casper 2000). Competition for light provides more competitive species with an  
68 increasing advantage as they outperform (i.e. become taller than) less competitive ones (Grime 1973a;

69 b; Huston & DeAngelis 1987; Grime 2001). When light is limiting, differentiation in light capture  
70 strategy (Bazzaz 1979) is required for species to co-exist (Aikio 2004; Kohyama & Takada 2009). In  
71 such instances, limiting similarity (i.e. competitive exclusion between species that are similar in their  
72 niche MacArthur & Levins 1967) should have a strong influence on community assembly processes,  
73 since divergence in light capture strategy will enhance species occurrence probability and abundance  
74 (Mason *et al.* 2011c). This will generate greater functional diversity in traits related to light capture  
75 strategy (Mouchet *et al.* 2010). Divergence in light capture strategy can be temporal (Grubb 1977;  
76 Bazzaz 1979; Huston & Smith 1987) or spatial (via vertical partitioning of light capture Botkin, Janak  
77 & Wallis 1972; Coomes *et al.* 2009). Species differing in regeneration niche are often divergent in  
78 resource use strategy. For example, short-lived gap exploiters have faster growth rates in high light  
79 conditions than shade-tolerant species (e.g. Horn 1974; Lieberman *et al.* 1985; Laurance *et al.*  
80 2004). The relationship between resource use strategy and regeneration niche may also drive differences  
81 in foliar traits between co-occurring species differing in longevity (Selaya *et al.* 2008; Easdale &  
82 Healey 2009). There is also evidence that vertical partitioning in light capture may also increase  
83 diversity in foliar traits, with sub-canopy species having a more resource-acquiring strategy than  
84 canopy species (e.g. Coomes *et al.* 2009).

85 In P-limited environments, where size symmetric below-ground competition dominates,  
86 competitive exclusion between species with similar niches may be less likely, since small differences in  
87 competitive ability will not have disproportionate effects on the outcome of competition (Rajaniemi  
88 2003). Coexistence between functionally similar species might also result from slower growth rates on  
89 nutrient-poor sites, reducing the pace of competition after disturbance (following the dynamic  
90 equilibrium theory of Huston 1979 and supported by experimental evidence; Rajaniemi 2003; Wardle  
91 & Zackrisson 2005). As a consequence, the influence of environmental filtering (i.e. when occurrence  
92 probability and abundance is enhanced by possession of traits similar to a locally "optimal" trait value

93 Mouillot, Mason & Wilson 2007; Mason *et al.* 2011c) should increase with declining soil fertility  
94 because occurrence probability and abundance will be enhanced by convergence on a resource  
95 retentive strategy (Lambers *et al.* 2008). Since there is no apparent mechanism to promote divergence  
96 in resource use strategy in P-limited environments, trait convergence between the most abundant  
97 species should occur.

98         Soil nutrient limitation may also influence species' light capture strategies. Coomes *et al.*  
99 (2009) demonstrated that sub-canopy tree species with a resource-acquiring strategy (e.g. high specific  
100 leaf area and nutrient content) were more abundant and captured a greater proportion of available light  
101 on a fertile site compared with a P-depleted one. This suggests that foliar trait divergence between  
102 canopy and sub-canopy trees increases with higher soil fertility. Similarly, low soil fertility might  
103 hinder divergence in regeneration niche (e.g. Coomes *et al.* 2009), by limiting maximum growth rates  
104 of gap colonisers in high light conditions. This would also constrain the potential for trait divergence  
105 among co-occurring species at low soil fertility.

106

## 107 FUNCTIONAL DIVERSITY INDICES AS INDICATORS OF ASSEMBLY PROCESSES

108 Functional diversity encompasses functional richness, functional evenness and functional divergence  
109 (Mason *et al.* 2005). Functional richness and functional divergence have most often been linked to  
110 community assembly processes (Mouchet *et al.* 2010; Mason *et al.* 2011b) or ecosystem functioning  
111 (Petchey, Hector & Gaston 2004; Mouillot *et al.* 2011), but one study demonstrated that functional  
112 evenness is also a potential indicator of assembly processes (Mason *et al.* 2008a). Modelling studies  
113 suggest that limiting similarity generates high functional richness and functional divergence, while  
114 environmental filtering reduces values for both components (e.g. Mouchet *et al.* 2010). Rao's quadratic  
115 entropy (Rao, henceforth) combines functional richness and divergence, and thus incorporates the two  
116 most powerful functional diversity components for detecting assembly processes. When using

117 occurrence data, Rao becomes highly sensitive to the volume of functional trait space occupied (i.e.  
118 functional richness). When observed Rao values are compared with those expected under null models  
119 that randomize species abundances within communities (as employed by Mason *et al.* 2008b; Vergnon,  
120 Dulvy & Freckleton 2009; Mason *et al.* 2011c), Rao becomes a pure index of functional divergence  
121 (Fig. S1). Higher Rao than expected at random provides evidence for limiting similarity, whereas lower  
122 Rao than expected is evidence for environmental filtering (Mason *et al.* 2011c).

123

## 124 AIMS AND OBJECTIVES

125 This study examines forest communities that represent a shift in the relative importance of light and  
126 nutrient competition along a soil chronosequence in the southern South Island of New Zealand. Light  
127 competition at our youngest study site has caused the exclusion of shade-intolerant pioneer species  
128 (Richardson *et al.* 2004). At the two oldest sites photosynthesis in all levels of the canopy is limited by  
129 low nutrient availability, with no evidence for light limiting growth in the sub-canopy (Tissue *et al.*  
130 2006) despite moderately high leaf area index at the second oldest site (mean of  $3.5 \text{ m}^2 \text{ m}^{-2}$  Walcroft *et al.*  
131 2005). We explore shifts in resource use strategy by examining changes in species means for foliar  
132 traits (leaf N and P, leaf thickness and density) used to contrast fast and leaky resource acquirers with  
133 slow and tight resource retainers (Cornelissen *et al.* 2003; Diaz *et al.* 2004; Wright *et al.* 2004). We  
134 then test whether convergence in resource use strategy is related to soil fertility by examining  
135 relationships between the functional richness, functional evenness and functional divergence of  
136 resource-use strategy traits and soil N and P content. This provides a test of whether mechanisms  
137 behind species co-existence change along fertility gradients.

138

## 139 Methods



## 140 STUDY AREA

141 The study area incorporates a series of schist glacial outwash surfaces and moraines between the Franz  
142 Josef Glacier and the coast in Westland, New Zealand. Eight sites (Table 1) spanning soil ages of 60 to  
143 120 000 years of soil exposure were chosen from Stevens (1968) and Almond *et al.* (2001). The sites  
144 occur between 43° 25' S and 43° 14' S latitude and between 170° 10' E and 170° 18' E longitude. The  
145 youngest six sites became exposed during glacial retreat following the last glacial maximum (c. 12, 000  
146 years b.p. Stevens 1968), while the two oldest sites are situated on moraines deposited from previous  
147 glacial maxima that have remained ice-free since their deposition (Almond *et al.* 2001). The climate in  
148 Westland is cool temperate (mean annual temperature 10.1 °C; (Hessel 1982) with an annual rainfall of  
149 c. 6500 mm year<sup>-1</sup> for the five youngest sites and c. 3500 mm year<sup>-1</sup> for the three oldest sites. The  
150 evergreen forests in this region typically contain mixtures of broadleaved angiosperm and long-lived  
151 coniferous tree species, (Wardle 1980; 1991), and have some of the highest biomass values in New  
152 Zealand (Mason *et al.* 2011a). For further details on sites see Stevens (1968) and Richardson *et al.*  
153 (2004).

154 The soil chronosequence provided by the eight study sites represents a strong gradient of  
155 declining total soil phosphorus (P) and pH. Total soil P and soil pH are highly correlated (Pearson's  $r =$   
156 0.9) across sites (Richardson *et al.* 2004), while soil total N exhibits a hump-backed relationship with  
157 site age. Soil data were taken from Richardson *et al.* (2004), who measured total mineral soil P, N and  
158 pH (see Blakemore, Searle & Daly 1987) from soils collected at each site during January 2002. While  
159 the youngest site (60 years) supports closed-canopy forest, the dominant species at this site do not  
160 regenerate beneath a closed canopy. The next youngest site (130 years) is dominated by canopy species  
161 typical of mature forest in the region (e.g. *Metrosideros umbellata* Myrtaceae, *Weinmannia racemosa*  
162 Cunoniaceae). This suggests that while differences between the youngest and second youngest sites  
163 may be due to primary succession, it is most likely that subsequent changes are due to declining soil

164 fertility. The six oldest sites are also likely to be affected by secondary succession through canopy tree  
165 mortality but these effects are minor at the stand scale relative to the effects of declining soil fertility  
166 through retrogression (Wardle *et al.* 2004; Peltzer *et al.* 2010). The sites are free from human  
167 disturbance, and there is no evidence of catastrophic disturbance has had a marked influence on current  
168 forest composition.

#### 169 LEAF TRAIT AND VEGETATION SAMPLING

170 Three circular plots of 10 m radius were randomly located at each site in February 2007. Within each  
171 plot we recorded species identity and stem diameter at 1.35 m height for all trees with stem diameter  $\geq$   
172 3 cm. Diameter measurements were used to calculate the basal area of each stem, and we recorded  
173 species abundance within each plot as the sum of individual basal areas.

174 Leaf trait data were collected during March 2002 at the end of the austral growing season. Whole  
175 branches were randomly taken from five individuals of each species at each site. Fully expanded sunlit  
176 leaves were collected where possible. Canopy branches were sampled using orchard cutters or a  
177 shotgun. Leaves were kept on branches, in plastic bags and in the dark until fresh leaf area could be  
178 measured using a LiCor Area Meter (Model Li-3100). Leaf thickness was measured using digital  
179 calipers; the midrib was avoided (Cornelissen *et al.* (2003) and the mean of three replicate leaves was  
180 used for each individual plant. Leaf mass was measured on material oven-dried at 60 °C for 48 h. Leaf  
181 volume was calculated from leaf area and leaf thickness and expressed relative to leaf mass to estimate  
182 leaf density. Biochemical analyses on dried material were made using the acid digest and colorimetric  
183 methods described in Blakemore *et al.* (1987). We chose to analyse patterns for four traits (Leaf N,  
184 Leaf P, thickness and density) since they are closely aligned to the global leaf economics spectrum  
185 (Wright *et al.* 2004), and thus are reliable indicators of plant resource use strategy. Leaf nutrient  
186 content and density are each related to maximum rates of photosynthesis per unit leaf dry weight  
187 (Niinemets 1999; Reich *et al.* 1999; Larcher 2003), while leaf thickness is positively related to

188 maximum photosynthetic rate per unit leaf area (Niinemets 1999). Also, leaf nutrient content is  
 189 negatively related, whereas leaf density and thickness (via their influence on SLA) positively related to  
 190 leaf longevity (Reich *et al.* 1999). Thus, the four traits we measured, when considered together,  
 191 document the trade-off between rapidly photosynthesizing species with short-lived leaves and those  
 192 with lower photosynthetic rates and longer-lived leaves.

193  
 194 FUNCTIONAL AND TAXONOMIC DIVERSITY CALCULATIONS

195 We used the FEve index of Villeger *et al.* (2008) to calculate functional evenness. This index involves  
 196 using a minimum spanning tree (MST) to estimate distances between nearest-neighbour species in  
 197 multivariate functional trait space. The functional regularity index (FRO) of Mouillot *et al.* (2005) is  
 198 then used to estimate functional evenness based on these distances in the MST. For simplicity we use  
 199 FEve<sub>Occ</sub> to indicate FEve calculated using occurrence data and FEve<sub>BA</sub> to indicate FEve calculated  
 200 using basal area data. Rao quadratic entropy was calculated following de Bello *et al.* (2009):

201 
$$\text{Rao} = \sum_{i=1}^S \sum_{j=1}^S d_{ij} p_i p_j ,$$

202 where  $S$  is species richness,  $d_{ij}$  the distance in functional trait space between species  $i$  and  $j$ , and  $p_i$  the  
 203 proportional abundance of species  $i$ . The distance between species was calculated using Gower's  
 204 dissimilarity, following Pavoine *et al.* (2009), which confines distances between species within the  
 205 bounds of 0 and 1:

206 
$$d_{ij} = \sum_{t=1}^T \frac{|x_{it} - x_{jt}|}{\max_t - \min_t} ,$$

207 where  $x_{it}$  is the value of trait  $t$  for species  $i$  and  $\max_t$  and  $\min_t$  the maximum and minimum values for  
 208 trait  $t$ . There are numerous options for defining maximum and minimum values for continuous traits.

209 We used the highest and lowest values observed across all our trait measurements. We calculated  $d_{ij}$   
 210 values either considering each trait separately (i.e. in one-dimensional functional trait space) or using  
 211 all four traits simultaneously (i.e. in four-dimensional trait space). We focus on results for Rao where  
 212  $d_{ij}$  is calculated using all traits simultaneously, since analyses for individual traits revealed qualitatively  
 213 similar patterns. Where relevant, analyses for Rao calculated using individual traits are referred to in  
 214 the text. Raw Rao values were converted to species richness equivalents (whereby Rao values are  
 215 expressed in the same units as species richness) following de Bello *et al.* (2010):

$$216 \quad \text{Rao}_{equiv} = \frac{1}{1 - \text{Rao}} .$$

217 Using this conversion, the value of Rao will be the same as the species richness equivalent for  
 218 Simpson's diversity if all  $d_{ij} = 1$ , and will be equal to species richness if all  $d_{ij} = 1$  and all species have  
 219 the same abundance. To express site mean Rao in number equivalents, we took the mean of raw Rao  
 220 values (calculated across plots within sites) and then applied the conversion to number equivalents. For  
 221 simplicity, we refer to Rao weighted by species occurrences as Rao<sub>Occ</sub> and to Rao weighted by basal  
 222 area as Rao<sub>BA</sub>. In all instances, both Rao<sub>Occ</sub> and Rao<sub>BA</sub> are expressed as species richness equivalents.

223 Estimation of taxonomic diversity was based on Simpson's concentration index:

$$224 \quad D = \sum_{i=1}^S p_i^2$$

225  $D$  was converted to a species richness equivalent measure of taxonomic diversity following the  
 226 conversion suggested by Jost (2007):

$$227 \quad D_{equiv} = D^{-1} .$$

228 Using this conversion,  $D_{equiv}$  is equal to species richness if all species have the same abundance. The  
 229 inverse Simpson's concentration index has long been used by ecologists as a measure of taxonomic

230 diversity, and its behaviour is well understood (Hill 1973). As for Rao, the mean of raw  $D$  values  
 231 was taken across plots within sites and then converted to number equivalents to provide a measure of  
 232 site mean taxonomic diversity. For brevity we refer to taxonomic diversity weighted by basal area as  
 233 Simpson diversity, although Jost (2007) demonstrates that various taxonomic diversity indices take the  
 234 same value for a given community following conversion to number equivalents. For Simpson diversity  
 235 weighted by occurrence data we refer simply to species richness, since this is equivalent to Simpson  
 236 diversity when all species have the same abundance.

237

#### 238 STANDARDISATION OF RAO VALUES RELATIVE TO RANDOM EXPECTATION

239 For the Monte Carlo standardization of Rao ( $Rao_{SES}$ ), expected Rao values were simulated by  
 240 randomizing relative abundances across species but within plots. This randomization retains all  
 241 processes that produced the observed data except those that affect species relative abundances (since  
 242 species occurrences remain constant). This method provides additional power to detect assembly  
 243 processes relative to co-occurrence-based simulation models, since species occurrences are controlled  
 244 by multiple factors (dispersal, interspecific competition and local environmental conditions). This may  
 245 confound efforts to reveal assembly processes by analysing co-occurrence (especially those based on  
 246 biotic interactions Mason *et al.* 2008b). A total of  $10^4$  randomizations were used in all analyses. For  
 247 each randomization, mean Rao across all plots within a site was calculated and then converted to  
 248 number equivalents in the same way as described for the observed data. For each site, observed Rao  
 249 was expressed relative to that expected by chance using the Standardized Effect Size (SES, Gotelli &  
 250 McCabe 2002):

$$251 \quad SES = \frac{Obs - Exp}{\sigma_{Exp}},$$

252 where Obs is the Rao value obtained from the observed data and Exp is the mean of the  
253 randomizations and  $\sigma_{Exp}$  the standard deviation of expected values. Positive SES values for Rao  
254 indicate the functional diversity is higher than expected with random distribution of abundances across  
255 species. This in turn suggests that the most abundant species in the plot tend to be more different from  
256 each other in their functional traits than expected by chance. For brevity, we refer to this expression of  
257 Rao as  $Rao_{SES}$  in the text and figures below.

## 258 CHANGES IN COMMUNITY STRUCTURE ALONG THE CHRONOSEQUENCE

259 Each of the diversity measures described above was regressed against total soil P and N. Soil  
260 pH was not included in the analyses due to its strong co-linearity with total soil P. Significance was  
261 assessed using jackknife (or “leave one out”) regression (Tukey 1958). Jackknife regression is suitable  
262 for small numbers of observations since it prevents a single observation from having a disproportionate  
263 influence on results. We also regressed the mean trait values of each species at each site and the  
264 abundance-weighted trait means of each plot against total soil P and N, using ordinary least squares  
265 regression. In all analyses, evidence for non-linear (logarithmic, quadratic and power) relationships was  
266 assessed using Akaike Information Criterion (AIC) weights (Burnham & Anderson 2002). The power  
267 relationship was defined as  $y = c + ax^b$ . The linear model was rejected if one of the non-linear models  
268 received a weight of  $>0.9$  (which would indicate a greater than 90% chance that the non-linear model  
269 was the most parsimonious, Burnham & Anderson 2002). The relative predictive ability of total soil N  
270 and P individually and in combination were also compared using AIC weights calculated across eight  
271 models: (1) total soil P only, (2) total soil N only, (3) both total soil P and N, (4) linear and quadratic  
272 terms for soil P, (5) linear and quadratic terms for soil N, (6) linear term for soil P and both linear and  
273 quadratic terms for soil N, (7) linear term for soil N and both linear and quadratic terms for soil P and  
274 (8) linear and quadratic terms for both soil N and soil P. AIC weights for each model ( $w_i$ ), were  
275 calculated using the method described by Johnson and Omland (2004):

276 
$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{j=1}^R \exp\left(-\frac{1}{2}\Delta_j\right)},$$

277 where  $R$  is the number of models under consideration and  $\Delta_i$  is the difference between the  $AIC_c$  value  
 278 of model  $i$  and the minimum  $AIC_c$  value across all models. The sum of  $w_i$  values across all models  
 279 adds to unity. The relative explanatory power of individual predictors across models was calculated by  
 280 summing the weights across each of the models in which it was included:

281 
$$w_k = \sum_{i=1}^{R_k} w_i,$$

282 where  $w_k$  is the AIC weight of predictor variable  $k$  and  $R_k$  is the number of models including  $k$  (this is  
 283 the same for all variables when all possible combinations of variables are examined). This weighting  
 284 provides a measure of the probability that a variable is in the set of the most parsimonious predictors.

285

## 286 Results

### 287 CHANGES IN BASAL AREA ALONG THE CHRONOSEQUENCE

288 Both mean and maximum basal area (taken across plots) were highest at the second youngest site (130  
 289 years, Table 1). Excluding the youngest site, mean basal area had a marginally significant negative  
 290 relationship with site age (Pearson's  $r = 0.69$ ,  $P = 0.042$ ) and a non-significant positive trend with  
 291 increasing total soil P (Pearson's  $r = 0.64$ ,  $P = 0.059$ ). Excluding the youngest site, maximum basal  
 292 area also had a marginally significant negative relationship with age (Pearson's  $r = 0.67$ ,  $P = 0.049$ )  
 293 and was significantly positively correlated with total soil P (Pearson's  $r = 0.71$ ,  $P = 0.036$ ). Thus there  
 294 is some evidence for a decline in basal area with site age and total soil P in sites older than 130 years.  
 295 In particular, basal area at the oldest site was markedly lower than all other sites  $\geq 130$  years old.

### 296 SHIFTS IN SPECIES TRAIT MEANS WITH SOIL P AND N

297 All ordinary least squares (OLS) regressions of species trait means on total soil P were significant  
298 and indicated a shift from a resource-retaining to resource-acquiring strategy with increasing soil P  
299 (Fig. 1, Table S1A). There was a linear increase in the leaf P of individual species (Fig. 1A) and a non-  
300 linear increase in leaf P (Fig. 1B), while leaf thickness showed a non-linear decline (Fig. 1D) with  
301 increasing soil P (Table S1A for results from all OLS models examined). For both leaf P and thickness,  
302 the Mitchell-Olds Shaw test for humps and pits (Mitchell-Olds & Shaw 1987) revealed no evidence for  
303 a change in gradient direction within the observed range of total soil P values, indicating that the  
304 observed quadratic relationships were monotonic. Leaf density decreased linearly with increasing soil P  
305 (Fig. 1C), though this relationship was weaker than for the other traits. Weighting regressions by  
306 species proportional abundances did not alter the shape of these relationships and all regressions  
307 remained significant (Table S1B). The results for weighted regressions indicate a general trend for the  
308 most abundant species to have a more resource retentive strategy as total soil P declined.

309 Quadratic relationships gave the best fits between soil N and species means for each of the four  
310 traits analysed in OLS regressions (Fig. 2, Table S1A). Weighted regressions did not qualitatively  
311 change the shape of relationships (compare values in Table S1A and B). The Mitchell-Olds Shaw test  
312 provided evidence for a change in the gradient for all regressions of soil N and species trait means  
313 (except weighted regression between soil N and leaf thickness), indicating that trait means did not vary  
314 monotonically with total soil N. Therefore, it is unlikely that variation in soil N is a major factor  
315 explaining variation in trait means along the entire gradient, although it may have an effect at older  
316 sites.

317 Soil P (or its quadratic term) received by far the highest AIC weights (leaf N, leaf P and  
318 thickness) of the four traits measured (Table S2), indicating it had the greatest explanatory power for  
319 these traits. Amongst the eight models compared, the model including only the linear soil P term  
320 received the highest AIC weight for leaf N and thickness while the quadratic soil P model received the



321 highest weight for leaf P (Table S1A). For leaf density, the model including linear terms for soil P  
322 and soil N and a quadratic term for soil P received the highest AIC weight (Table S1A). Multi-model  
323 comparison results were very similar for weighted regression (Table S2B). Overall, it appears that  
324 except for leaf density, the inclusion of soil N data did not improve our ability to predict species trait  
325 means, irrespective of whether or not regressions were weighted by abundance.

326

### 327 SHIFTS IN FUNCTIONAL AND TAXONOMIC DIVERSITY WITH SOIL P AND N

328 There was no relationship between species richness,  $Rao_{occ}$ ,  $FEve_{occ}$  and soil P, when each trait was  
329 considered separately or all traits were considered simultaneously (Fig. 3). This indicates that  
330 functional richness, woody plant species richness, functional richness and regularity of species  
331 distribution in functional trait space were unrelated to soil P. There was a strong positive relationship  
332 between  $Rao_{SES}$  and soil P (Fig. 4D) and this relationship was strongly significant using jackknife  
333 regression. This result indicates that functional divergence was strongly positively correlated with soil  
334 P (Fig. S1), which suggests that the dominant species at high fertility sites had complementary trait  
335 values, while those at low fertility sites converged on similar trait values. Simpson diversity,  $FEve_{BA}$   
336 and  $Rao_{BA}$  values were unrelated to soil P (Fig. 4). Figure 5 provides examples of plots with the  
337 highest and lowest values of  $Rao_{SES}$  for the four traits measured. For each trait it is clear that in the  
338 plots with the lowest  $Rao_{SES}$  value the most abundant species all have very similar trait values (relative  
339 to the mean distance between species), while in the plots with the highest values the most abundant  
340 species have quite different values.

341 When each of the traits was considered separately,  $Rao_{SES}$  values were significantly positively  
342 correlated with soil P in jackknife linear regression for leaf N and P, but not for leaf density or  
343 thickness. However, the relationship for any single trait was not as strong as when all four traits were

344 analysed together. This suggests that rather than primarily being driven by any single trait, there is a  
345 coordinated trait syndrome towards nutrient conservation with declining soil resource availability.  
346  $RaO_{BA}$  values were not significantly related to soil P for any single trait in jackknife regression (data  
347 not shown), though there was a significant positive linear relationship in OLS regression for leaf N and  
348 leaf P.

349         There was no evidence for non-linear relationships between any of the diversity measures used  
350 and soil P. The addition of linear or quadratic terms for total soil N provided no improvement in  
351 predictive ability for any of the diversity measures.

352

## 353 Discussion

354 The monotonic declines in species mean leaf N and P and the increases in leaf thickness and density  
355 that accompanied declining soil P indicate a shift from a resource-acquiring strategy (with fast growth  
356 rates, high nutrient investment in leaves and reduced leaf longevity) on the most fertile sites to a  
357 resource-retaining strategy on the least fertile sites. Very similar results were obtained when  
358 abundance-weightings were applied, indicating that both abundant and rare species become more  
359 resource retaining as soil P declines.  $RaO_{SES}$  (abundance-weighted Rao expressed relative to random  
360 expectation), was the only measure of functional or taxonomic diversity significantly related to total  
361 soil P. Its steep decline with decreasing soil P along the chronosequence indicates that locally dominant  
362 species became much more convergent in their resource use strategy as soil fertility decreased (i.e.  
363 there was a steep decline in functional divergence; Fig. S1A). This provides evidence that the  
364 mechanisms for species co-existence change along fertility gradients, with niche differentiation in  
365 resource use strategy required for co-existence at high fertility but not at low fertility. Below, we  
366 discuss our results with reference to the ecology of the species studied. We also consider the relevance  
367 of our work for the potential of functional diversity indices to reveal assembly processes.

368

## 369 DECLINING SOIL P AND SPECIES RESOURCE USE STRATEGY

370 The monotonic shift from a resource-acquiring to an extreme resource-retaining strategy suggests that  
371 vegetation change along the chronosequence is driven primarily by a decline in soil P (see also  
372 Richardson *et al.* 2004; Wardle *et al.* 2004; Peltzer *et al.* 2010). In contrast, the general lack of  
373 monotonic relationships between soil N and species trait means suggests that soil N was not a major  
374 factor in driving trait variation. Indeed, soil N generally did not add to the explanatory power provided  
375 by soil P (Table S1). It should be noted that soil pH was strongly correlated with soil P across the sites  
376 studied. However, pH was relatively invariant from the middle-aged to oldest sites in the  
377 chronosequence (Table 1), and considerable shifts in leaf N, P and thickness were observed between  
378 these sites (Fig. 1). This suggests that low pH was not the primary factor driving the extreme resource-  
379 retaining strategy of species at the oldest, least fertile sites.

380 The observed shifts in species resource use strategy were due both to changes in species  
381 composition and variation within species occurring at multiple sites. Resource-retaining conifers (e.g.  
382 *Dacrydium cupressinum*, Podocarpaceae) and angiosperms (e.g. *Quintinia acutifolia*, Escalloniaceae)  
383 increased in relative abundance with declining soil P. The youngest, most fertile sites contained a  
384 variety of relatively fast growing angiosperm tree species that exploit canopy gaps (e.g. *Melicytus*  
385 *ramiflorus*, Violaceae, and *Carpodetus serratus*, Escalloniaceae) and may persist at relatively high  
386 abundance for more than 200 years in the canopy or sub-canopy following secondary succession  
387 (Mason *et al.* 2011b). Also present at the most fertile sites are species with high nutrient, thin, low-  
388 density leaves which occur in reasonable abundance in the canopy or sub-canopy of mature forest (e.g.  
389 the angiosperms *Schefflera digitata* and *Raukaua simplex*, Araliaceae, and the tree fern *Cyathea*  
390 *smithii*, Cyatheaceae). These species were conspicuously absent from older, less fertile sites. Even on  
391 the most fertile sites the most abundant species tended to have a resource-retaining strategy relative to

392 co-occurring species. This could be due to limitations in the regional species pool, which lacks  
393 canopy dominants with a resource-acquiring strategy (McGlone, Richardson & Jordan 2010). Previous  
394 work (Richardson *et al.* 2005) has demonstrated that, for the vast majority of species studied,  
395 intraspecific variation in leaf nutrient concentrations is strongly related to variation in soil P between  
396 sites. The contribution of intraspecific variation to the observed shifts in species trait means highlights  
397 the need to obtain trait measurements for each species from all the sites where it occurs, rather than  
398 applying a single trait value to each species (Shipley, Vile & Garnier 2006).

399

#### 400 FUNCTIONAL DIVERSITY AND CO-EXISTENCE – ECOLOGICAL CONSIDERATIONS

401 Our results provide strong evidence for a decline in functional divergence with declining soil P, driven  
402 by the most abundant species within local communities converging in their resource use strategy (Fig.  
403 4). It is likely that size-asymmetric competition for light at high fertility sites means that differentiation  
404 in light capture strategy is required for species' co-existence. Canopy gaps provide an opportunity for  
405 temporal differentiation in light capture (i.e. between canopy dominants and gap colonisers, Grubb  
406 1977; Brokaw 1985), while spatial differentiation occurs vertically, with sub-canopy species adapted to  
407 grow and reproduce in low light levels (Coomes *et al.* 2009). At our most fertile sites, both the gap  
408 colonisers and shade-tolerant sub-canopy species have foliar traits typical of resource-acquiring  
409 strategists, which contrast with the resource-retaining traits of the co-occurring canopy dominant  
410 species. This increases functional divergence, since it leads to a situation where the most abundant  
411 species have quite different trait values. Declining nutrient availability excluded or greatly reduced the  
412 abundance of fast-growing species that exploit gaps and shade-tolerant species having resource-  
413 acquiring leaf traits, thus reducing functional divergence.

414 Species abundances in P-limited environments are generally enhanced by the ability to  
415 acquire nutrients at low concentrations in the soil solution and to retain nutrients (e.g. Lambers *et al.*  
416 2008). Consequently, only species with a resource retaining strategy are likely to achieve high  
417 abundance in P-limited environments. For this chronosequence, Richardson *et al.* (2005) demonstrated  
418 consistent increases in litter nutrient resorption efficiency with declining soil P across species.  
419 Similarly, Holdaway *et al.* (2011) showed that root traits shifted in a coordinated way for enhanced  
420 nutrient absorption and increased root longevity on low fertility sites (i.e. relatively high specific root  
421 length (ratio of root length to root dry mass), high root tissue density, and low root nutrient  
422 concentrations. Our results for changes in species trait means and functional divergence, combined  
423 with those of Richardson *et al.* (2005) and Holdaway *et al.* (2011), emphasise the increasing  
424 importance of greater efficiency in nutrient scavenging and retention for dominance as soil P declines.  
425 The link between a resource retentive strategy and chemical anti-herbivore defence has long been  
426 established, with chemical defences often assumed to be an adaptation which allows retentive species  
427 to limit tissue loss and thus conserve nutrient resources (e.g. Coley 1987). Previous work has  
428 demonstrated that the coniferous species which dominate the least fertile sites in our study have very  
429 high levels of anti-herbivore defence compounds (data presented in Mason *et al.* 2010). This further  
430 emphasises the importance of adopting a resource-retaining strategy for dominance in P-limited  
431 environments.

432 Some authors have suggested that the importance of facilitation for co-existence might increase  
433 with stress, including reduced nutrient availability (Callaway & Walker 1997; Michalet *et al.* 2006).  
434 This could in turn increase functional diversity, because facilitation enhances functional  
435 complementarity between species. However, studies of facilitation in response to nutrient stress mainly  
436 examine evidence for positive effects of N-fixing species on co-occurring non-N-fixers in N-limited  
437 environments (e.g. Walker & Chapin 1986; Morris & Wood 1989; Huston 1994; Marleau *et al.* 2011),

438 and we are unaware of any evidence for facilitation in P-limited environments. The increasing trait  
439 convergence between dominant species with declining soil P may partly reflect the lack of potential for  
440 differentiation in resource use strategy to enhance abundance at P-limited sites. The maintenance of  
441 taxonomic diversity (expressed as either species richness or species diversity) at the oldest sites may  
442 depend partly on the size-symmetric nature of nutrient competition, which makes competitive  
443 exclusion between species more difficult (Rajaniemi 2003; Wardle & Zackrisson 2005; Gundale *et al.*  
444 2011). This will increase the likelihood of co-existence between species with similar resource use  
445 niches (Huston 1979). It is possible that resource partitioning of P (i.e. adaptation for use of P sources  
446 requiring more or less investment for uptake) might also permit co-existence when P is limiting (Turner  
447 2008), and this might not necessarily manifest itself in foliar or root trait divergence.

448

#### 449 FUNCTIONAL DIVERSITY AND CO-EXISTENCE – METHODOLOGICAL CONSIDERATIONS

450 The method used to express functional diversity values can have a large effect on the patterns observed.  
451 Rao expressed relative to that expected when species abundances are randomly allocated within  
452 communities was the only functional diversity measure to decline significantly with declining total soil  
453 P. Rao expressed in this way is a pure index of functional divergence. The randomisation approach we  
454 employed has been used in a previous study to reveal changes in niche overlap in response to  
455 experimental treatments and the biomass gradient they create in a meadow plant community (Mason *et*  
456 *al.* 2011c). It has also proven a powerful means of revealing community assembly processes in  
457 lacustrine fish communities (Mason *et al.* 2008b) and a marine phytoplankton community (Vergnon *et*  
458 *al.* 2009). These studies, and our findings, suggest that this randomisation method can be applied to a  
459 broad range of ecological contexts, for example, detecting trait convergence with declining  
460 productivity. Further, our study demonstrates that detecting changes in the functional diversity of plant  
461 communities along gradients requires an objective estimate of species abundances; here we used tree

462 basal area, a proxy for plant biomass. Relative abundance gives an indication of species' ability to  
463 acquire resources under local environmental conditions and in competition with co-occurring species  
464 (Whittaker 1965; Grime 2001). Consequently, linking functional traits and abundance to estimate  
465 functional diversity may reveal the consequences of trait convergence and divergence for resource  
466 acquisition in local communities, which will in turn help to reveal changes in co-existence mechanisms  
467 along ecological gradients.

468

## 469 CONCLUSIONS

470 Our findings suggest that the mechanisms behind species co-existence change along long-term soil  
471 fertility gradients. At high fertility, size-asymmetric competition for light means that differentiation in  
472 resource-use strategy is required for species co-existence. At low fertility, size-symmetric competition  
473 for nutrients permits species with similar resource use strategy to co-exist. Our study also demonstrates  
474 that quantifying trait convergence and divergence with functional diversity indices can complement the  
475 information provided by taxonomic diversity and functional composition to improve our understanding  
476 of changes in assembly processes along environmental gradients. We suggest that functional diversity  
477 indices should be added to the standard toolkit that ecologists use in studying vegetation change along  
478 gradients of environmental stress and ecological succession. Doing so has great potential to improve  
479 our understanding of the processes driving vegetation change along environmental gradients.

480

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486

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683 **Table 1.** Age, mean and maximum basal area in circular plots of 10 m radius in total soil nitrogen and phosphorous (total N and total P),  
 684 pH, number of species with trait measurements, mean species richness (taken across plots) and the dominant species (measured by basal  
 685 area) for each of the sites studied.

Age (years)	Mean Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Max Basal Area (m <sup>2</sup> ha <sup>-1</sup> )	Total N (g kg <sup>-1</sup> )	pH	Total P (mg kg <sup>-1</sup> )	Species measured	Mean species richness	Dominant species
60	34	37	2.21	5.6	805	13	6.3	<i>Griselinia littoralis</i>
130	141	258	3.74	4.6	554	13	6.4	<i>Metrosideros umbellata</i> , <i>Weinmannia racemosa</i>
280	118	136	6.08	4.4	514	14	9.3	<i>Metrosideros umbellata</i> , <i>Weinmannia racemosa</i>
530	70	98	8.02	4.0	458	15	8.9	<i>Metrosideros umbellata</i> , <i>Weinmannia racemosa</i>
5000	107	156	4.99	3.9	351	13	6.4	<i>Dacrydium cuppresinum</i> , <i>Weinmannia racemosa</i>
12 000	102	130	6.93	3.9	327	15	7.1	<i>Weinmannia racemosa</i> , <i>Dacrydium cuppresinum</i> , <i>Metrosideros umbellata</i>
60 000	112	119	3.37	3.9	201	13	8.6	<i>Metrosideros umbellata</i> , <i>Dacrydium cuppresinum</i> , <i>Weinmannia racemosa</i>
120 000	33	40	3.56	3.9	108	10	8.0	<i>Dacrydium cuppresinum</i> , <i>Phyllocladus alpinus</i> , <i>Podocarpus totara</i>

686

687 **Fig. 1.** Regression of four key leaf traits (Leaf phosphorus, A; Leaf nitrogen, B; Leaf density, C;  
 688 Leaf thickness, D) on total soil phosphorus along a long-term soil chronosequence. Each circle  
 689 represents the mean of measurements for a single species at a single site. Diameter of circles is  
 690 proportional to species' mean proportional abundance (across plots within sites). The solid lines  
 691 indicate relationships fitted using ordinary least squares (OLS) regression, while the dashed lines  
 692 indicate relationships fitted using weighted least squares regression in which species' mean  
 693 proportional abundances were used as weights. Circles for all species with proportional abundance  $\leq 0.1$   
 694 have the same diameter.

695

696 **Fig. 2.** Regression of four key leaf traits (Leaf phosphorus, A; Leaf nitrogen, B; Leaf density, C; Leaf  
 697 thickness, D) on total soil nitrogen along a long-term soil chronosequence. Each circle represents the  
 698 mean of measurements for a single species at a single site. Diameter of circles is proportional to species'  
 699 mean proportional abundance (across plots within sites). The solid lines indicate relationships fitted  
 700 using ordinary least squares (OLS) regression, while the dashed lines indicate relationships fitted using  
 701 weighted least squares regression in which species' mean proportional abundances were used as  
 702 weights. Circles for all species with proportional abundance  $\leq 0.1$  have the same diameter.

703 **Fig. 3.** Mean (across plots within sites) species richness (A), and functional evenness (FEve, B) and  
 704 Rao (C) using presence/absence data ( $Rao_{Occ}$ ) for each site along the chronosequence versus total soil P.  
 705  $Rao_{Occ}$  values are expressed as species richness equivalents following de Bello *et al.* (2010). OLS  $R^2$  is  
 706 the R-square value from ordinary least squares regression. <sup>NS</sup> indicates the regression is not significant  
 707 ( $P > 0.1$ ).

708 **Fig. 4.** Mean (across plots within sites) basal area-weighted Simpson diversity (A), functional evenness  
 709 (FEve, B) and Rao ( $Ra_{OBA}$ , C) and Rao expressed relative to random expectation ( $Ra_{SES}$ , D) for each

710 site along the chronosequence versus total soil P. Each point represents a single site along the  
711 chronosequence. Simpson diversity is the inverse of Simpson's concentration index, and is expressed as  
712 species richness equivalents following Jost (2007).  $Rao_{BA}$  values are expressed as species richness  
713 equivalents following de Bello *et al.* (2010).  $Rao_{SES}$  is observed  $Rao_{BA}$  expressed relative to random  
714 expectation using the Standardised Effect Size (SES) of Gotelli and McCabe (2002). OLS  $R^2$  is the R-  
715 square value from ordinary least squares regression. <sup>NS</sup> indicates the regression is not significant ( $P >$   
716 0.1).

717

718 **Fig. 5.** Examples of plots with the highest and lowest values of  $Rao_{SES}$  for each of the four traits  
719 studied (Leaf phosphorus, A; Leaf nitrogen, B; Leaf density, C; Leaf thickness, D). In each of the  
720 figures, open circles indicate species occurring in a plot with a low  $Rao_{SES}$  value while filled circles  
721 indicate species from a plot with a high  $Rao_{SES}$  value.  $Rao_{SES}$  is observed basal area weighted Rao  
722 ( $Rao_{BA}$ ) expressed relative to random expectation using the Standardised Effect Size (SES) of Gotelli  
723 and McCabe (2002).

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