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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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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^{-1}). 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

Introduction

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

COMPETITION, SOIL FERTILITY AND TRAIT DIVERGENCE

Long-term soil chronosequences embody strong soil fertility (primarily phosphorus, P) gradients (Walker & Syers 1976; Richardson *et al.* 2004), and a concomitant shift from light to soil nutrient limitation of plant growth (e.g. Coomes & Grubb 2000). Competition for light is size-asymmetric whereas competition for nutrients is size-symmetric (Schwinning & Weiner 1998; Berntson & Wayne 2000; Cahill & Casper 2000). Competition for light provides more competitive species with an 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 $m^2\,m^{-2}$ Walcroft *et*

131   *al.* 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^{-1} for the five youngest sites and *c*. 3500 mm year^{-1} 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 ≥

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 $FEve_{Occ}$ to indicate FEve calculated using occurrence data and $FEve_{BA}$ 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 $$d_{ij} = \sum_{t=1}^{T} \frac{\left| x_{it} - x_{jt} \right|}{\max_t - \min_t} \,,$$

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

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_{Occ} and to Rao weighted by basal

222 area as Rao_{BA}. In all instances, both Rao_{Occ} and Rao_{BA} are expressed as species richness equivalents.

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

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

225 D was converted to a species richness equivalent measure of taxonomic diversity following the

226 conversion suggested by Jost (2007):

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

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

252   where Obs is the Rao value obtained from the observed data and Exp is the mean of the

253   randomizations and σ_{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 $\mathrm{Rao_{SES}}$ 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
$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum\limits_{j=1}^{R}\exp\left(-\frac{1}{2}\Delta_j\right)},$$

277 where R is the number of models under consideration and Δ_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 ≥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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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^2ha^{-1})	Max Basal Area (m^2ha^{-1})	Total N ($g\,kg^{-1}$)	pH	Total P ($mg\,kg^{-1}$)	Species measured	Mean species richness	Dominant species
60	34	37	2.21	5.6	805	13	6.3	*Griselinia littoralis*
130	141	258	3.74	4.6	554	13	6.4	*Metrosideros umbellata, Weinmannia racemosa*
280	118	136	6.08	4.4	514	14	9.3	*Metrosideros umbellata, Weinmannia racemosa*
530	70	98	8.02	4.0	458	15	8.9	*Metrosideros umbellata, Weinmannia racemosa*
5000	107	156	4.99	3.9	351	13	6.4	*Dacrydium cuppresinum, Weinmannia racemosa*
12 000	102	130	6.93	3.9	327	15	7.1	*Weinmannia racemosa, Dacrydium cuppresinum, Metrosideros umbellata*
60 000	112	119	3.37	3.9	201	13	8.6	*Metrosideros umbellata, Dacrydium cuppresinum, Weinmannia racemosa*
120 000	33	40	3.56	3.9	108	10	8.0	*Dacrydium cuppresinum, Phyllocladus alpinus, Podocarpus totara*

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 ≤ 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 ≤ 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. [NS] 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 (Rao_{BA}, C) and Rao expressed relative to random expectation (Rao_{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, an 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. [NS] 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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