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PREPRINT

1   **Running head**: Diversity, rooting depth, and productivity

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3   **Title:** Root depth distribution and the diversity-productivity relationship in a long-term grassland

4   experiment

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24 **Abstract**

25 The relationship between plant diversity and productivity in grasslands could depend, partly, on

26 how diversity affects vertical distributions of root biomass in soil; yet, no prior study has

27 evaluated the links among diversity, root depth distributions, and productivity in a long-term

28 experiment. We use data from a 12-year experiment to ask how plant species richness and

29 composition influenced both observed and expected root depth distributions of plant

30 communities. Expected root depth distributions were based on the abundance of species in each

31 community and two traits of species that were measured in monocultures: root depth

32 distributions and root to shoot ratios. The observed proportion of deep root biomass increased

33 more than expected with species richness and was positively correlated with aboveground

34 productivity. Indeed, the proportion of deep root biomass explained variation in productivity

35 even after accounting for legume presence/abundance, and greater nitrogen availability in diverse

36 plots. Diverse plots had root depth distributions that were twice as deep as expected from their

37 species composition and corresponding monoculture traits, partly due to interactions between C4

38 grasses and legumes. These results suggest the productivity of diverse plant communities was

39 partly dependent on belowground plant interactions that caused roots to be distributed more

40 deeply in soil.

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42 **Keywords**: root biomass, aboveground biomass, complementarity, legume, C4 grass, species

43 richness, interspecific interactions

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47   **Introduction**

48   The positive diversity-productivity relationship in experimental grasslands is facilitated,

49   partly, by greater capture of soil resources in more diverse plant communities (Tilman et al.

50   1996, Scherer-Lorenzen et al. 2003, Spehn et al. 2005, Fornara and Tilman 2009). Several

51   factors can enhance resource acquisition in diverse plant communities, including: i) the presence

52   of nitrogen-fixing legumes (Spehn et al. 2002); ii) positive feedbacks from plant productivity and

53   plant nutrient concentrations to soil nutrient availability (Fornara and Tilman 2009, Reich et al.

54   2012); iii) high root biomass and root activity (Tilman et al. 1996, de Kroon et al. 2012); and iv)

55   niche differentiation with respect to resource requirements and extraction (Berendse 1982,

56   Mckane et al. 1990, Fargione and Tilman 2005a, von Felten et al. 2009). In this paper, we focus

57   on one related, but under-studied, factor that could greatly influence soil resource use and

58   partitioning: the vertical distribution of roots in soil.

59   The vertical distribution of roots could influence the amount and complementarity of soil

60   resource extraction in two ways. First, combinations of species with *inherently* different rooting

61   distributions, for example shallow and deep-rooted species, could facilitate coexistence and more

62   exhaustive use of soil resources (Berendse 1982, Mommer et al. 2010). Second, *adjustments* in

63   root:shoot ratios or rooting depths by one or more species in a community could facilitate

64   coexistence and increase total resource extraction. For instance, in response to depletion of

65   surface soil resources in diverse communities, some species might allocate more root biomass to

66   deep soil (Fargione and Tilman 2005b, Schenk 2008, Skinner and Comas 2010). Species in

67   diverse communities might also alter the depth distribution of roots in response to the density

68   and identity of neighboring roots (Schenk 2006, Mommer et al. 2010, de Kroon et al. 2012).

69   In this study, we explore the relationships among plant diversity, root depth distributions,

70   and productivity using data from the 12th year of a grassland plant diversity experiment (Tilman

71   et al. 2001). First, we evaluate how root depth distributions, at the community level, are

72   influenced by plant species richness and the presence and abundance of plants from different

73   functional groups. We then assessed the implications of community-level root depth distributions

74   for the diversity-productivity relationship. Previous studies of this experiment showed that both

75   above- and belowground plant biomass were positively correlated with plant species richness.

76

77   **Methods**

78   *Study site.* The experiment, located near Bethel, Minnesota (USA), was initiated in 1993

79   and planted in 1994 (Tilman et al. 2001). For the growing season, approximately May thru

80   September, the average maximum daily temperature between 1994 and 2006 was 24.4 °C, the

81   average minimum temperature was 11.7 °C, and the average precipitation was 480 mm. Soils are

82   derived from glacial outwash and have coarse texture (>90% sand). Percent carbon and nitrogen

83   (N) in soil are typically lower than 1% and 0.1%. The upper 6 to 8 cm of soil was removed prior

84   to seeding. Plots (9 m x 9 m) were seeded to achieve five different levels of plant species

85   richness (1, 2, 4, 8, and 16 species). Each level of species richness was replicated more than 25

86   times. Species composition of each plot was determined by random draws from a pool of 18

87   plant species that included four non-legume forbs (hereafter forbs), four non-woody legumes,

88   four C3 grasses, four C4 grasses, and two *Quercus* species. Thus, all 16-species plots contain at

89   least two species from each of the herbaceous plant types. All plots were ignited in the spring of

90   each year and weeded ~3 times per year to remove non-planted species. Following Tilman et al.

91   (2006), we focus on 152 plots that burn well and have very little *Quercus* biomass.

92   *Sampling.* In August 2006, we sampled root biomass in three different depth increments,

93   0-30 cm, 30-60 cm, and 60 to 100 cm. Three soil cores, five cm in diameter, were removed and

94   composited for each plot before roots were isolated from the soil by rinsing with water over a

95   1.5-mm mesh screen. Roots were dried at 40 °C for 10 days and weighed (Fornara and Tilman

96   2008). Aboveground biomass was sampled in August and it approximates aboveground

97   productivity due to annual spring burning (Tilman et al. 2006).

98   *Estimating net adjustments of rooting depth in multi-species communities.* For each plant

99   species and each rooting depth increment (0-30, 30-60 and 60-100 cm), we calculated the ratio of

100   root biomass to aboveground biomass using data from the monoculture plots of each species.

101   Then, for each species in a multispecies plot, the monoculture-derived root:shoot ratios were

102   multiplied by the relative aboveground abundance of that species in the mixture (i.e. the

103   proportion of total aboveground biomass attributed to that species). Finally, the calculated root

104   biomass values for each species in a plot were summed to produce an "expected" root depth

105   distribution for each plot. The expected root depth distributions reflect a null hypothesis for each

106   experimental plant community, based on the null expectation that species do not adjust their

107   root:shoot ratios or root depth distributions in response to changes in community composition or

108   resource availability. Consequently, deviations of observed root depth distributions from

109   expected values reflect adjustments in rooting depth and/or root:shoot ratios of individual species

110   that cause the root depth distribution of the whole community to become deeper, or more

111   shallow, than expected based on community composition and monoculture traits.

112   We estimated the expected root depth distributions for a subset of plots dominated by

113   species with well-characterized root depth distributions in monoculture. We defined well-

114   characterized species as those for which >70% of aboveground biomass in monoculture plots

115   was derived from the target species. Twelve of the 16 focal species met this criterion; two C3

116   grasses, including *Poa pratensis*, and two forbs did not meet this criterion. However, we have

117   confidence in our estimate of the root depth distribution of *Poa pratensis* monocultures because a

118   similar value, within 1% of our estimate, was observed in a neighboring experiment (P.B. Reich

119   unpublished). Expected root depth distributions were then calculated for plots where > 70% of

120   the aboveground biomass was accounted for by these thirteen species (137 out of 152 plots).

121   More and less strict cutoffs yielded similar results.

122   *Statistics.* All data were assessed for normality and transformed accordingly, frequently

123   using a square-root transformation. We then used ANOVA models with different combinations

124   of factors to tease out their effects on dependent variables. Type III sums of squares were used

125   for significance tests, such that the contribution of each factor was evaluated *after* accounting for

126   the effects of the other predictors (Hector et al. 2010). Community functional composition was

127   evaluated using binary variables coded for the presence/absence of different plant functional

128   groups (e.g. legumes, C4 grasses). To assess the effects of individual species, we used separate

129   analyses with binary variables coded for the presence/absence of each of the 13 focal species

130   (species richness was not included as a covariate). Finally, to build on previous studies that

131   identified plant N concentrations and soil N availability as important predictors of productivity in

132   our experiment (Fargione et al. 2007; Fornara & Tilman, 2009), we compared the effect of root

133   depth distributions and N-related parameters on aboveground biomass and total root biomass in

134   additional regression models. All analyses were performed using JMP (©SAS Institute Inc.).

135

136   **Results**

137   *Depth distribution of root biomass.* Across all plots, the upper 30 cm of soil contained

138   between 51 and 100% of the total root biomass (sampled to a depth of 1 m). Root biomass in the

139   30 to 60 cm and 60 to 100 cm depth increments showed similar patterns with species richness

140   (Fig. A1 in Appendix A) and community composition (not shown), so for statistical analyses we

141   combined these two depth increments into one: root biomass between 30 and 100 cm.

142   Planted species richness was positively correlated with root biomass in the surface soil

143   (0-30 cm; R^2=0.43, P<0.0001) and in the deeper soil (30-100 cm; R^2=0.34, P<0.0001), even after

144   accounting for variation in the presence of different functional groups (Table A1 in Appendix

145   A). Species richness had a greater positive effect on deep root biomass; the median root biomass

146   below 30 cm was ~7 times higher in 16-species plots than in monocultures, while the median

147   root biomass in the upper 30 cm of soil was ~3.5 times higher in 16-species plots as compared to

148   monocultures. Consequently, species richness had a positive effect on the proportion of total root

149   biomass present below 30 cm (hereafter, the deep root proportion; P<0.001; Table A2; Fig. 1C).

150   The effects of plant functional composition on root biomass at different depths were

151   consistent with patterns observed in monocultures. Among monocultures, legumes had the

152   deepest rooting systems, with more than 20% of root biomass typically below 30 cm (Table A3).

153   Considering all plots, the presence of legumes was associated with higher root biomass in each

154   depth increment, especially in the 30 to 100 cm increment (P<0.001, Table A1), such that plots

155   with legumes had higher deep root proportions (P<0.0001; Table A2). For example, the deep

156   root proportion in mixtures with legumes was 3 times larger than in mixtures without legumes

157   (Fig. 1G). Contrastingly, C3 grasses had the shallowest root systems among monocultures, with

158   typically less than 1% of total root biomass occurring below 30 cm (Table A3). Accordingly,

159   across all plots, the presence of C3 grasses had negative effects on both deep root biomass

160   (P=0.01, Table A1) and the deep root proportion (P<0.01; Table A2). In monocultures, C4

161   grasses and forbs had intermediate and more species-specific depth distributions of root biomass

162   (Table A3), while across all plots the presence of C4 grasses and forbs had no main effect on the

163   deep root proportion (Table A2). For models of root biomass and deep root proportion, there

164   were significant interaction terms related to plant functional composition; but, species richness

165   and the main functional group effects typically explained more variation, i.e. had higher type III

166   sums-of-squares, and had smaller P values (Tables A1 and A2).

167   *Expected vs. observed root depth distributions*. The differences between observed and

168   expected root depth distributions, which we expressed as differences between observed and

169   expected deep root proportions, were also related to species richness and functional composition.

170   The observed deep root proportion in the most diverse plots was two times higher than the

171   expected value (26% vs. 13%; $P<0.0001$). The deep root proportion for plots planted with eight

172   species was 33% higher than expected (19% vs 14%; $P<0.05$), whereas observed and expected

173   deep root proportions were not significantly different for lower levels of species richness (Fig.

174   1D; significance was evaluated using paired-t tests). The co-occurrence of legumes and C4

175   grasses was strongly associated with higher deep root proportions than expected ($P≤0.001$; Table

176   A4). Most diverse plots contained both of these plant types, but species richness had a significant

177   effect on the deviations from expected deep root proportions even when legume and C4 grass

178   presence were included as covariates ($P<0.001$; Table A4). Also, when comparing among plots

179   with at least one legume and C4 grass present, the deviations from expected deep root

180   proportions were larger for 16-species plots than for plots with 8 or less species (Fig. 1H). The

181   presence of forbs and C3 grasses was associated with deep root proportions that were lower than

182   expected, but only when species richness was included as a covariate ($P<0.05$; Table A4).

183   *Effects of individual plant species. Lupinus perennis*, *Lespedeza capitata* and *Amorpha*

184   *canascens* each had significantly positive effects on the deep root proportion ($P<0.01$), but the

185 presence of *Petalostemum purpureum* was not a significant factor. According to calculations

186 based on model coefficients, the deep root proportion increased by 17% when *Lupinus perennis*

187 was present, compared to 5 and 6% when *Lespedeza capitata* and *Amorpha canascens* were

188 present. The presence of other species did not have apparent effects on the deep root proportion.

189 The presence of *Lespedeza capitata*, *Lupinus perennis*, and *Schizachyrium scoparium* (a C4

190 grass) were associated with higher deep root proportions than expected ($P<0.05$), with the

191 predicted effect sizes (using model coefficients) of *Lupinus perennis* and *Schizachyrium*

192 *scoparium* more than double that of *Lespedeza capitata*. None of the species were linked with

193 lower than expected deep root proportions based on their presence/absence.

194   *Covariance of root depth distributions and plant biomass.* Across all levels of species

195 richness, both aboveground and belowground biomass were positively correlated with deep root

196 proportion (R^2=0.31 and 0.24, respectively, $P<0.0001$, n=152) and with the difference between

197 observed and expected deep root proportions (R^2=0.19 and 0.37, respectively, $P<0.0001$, n=137).

198 Since deep root proportions were strongly positively correlated with the differences between

199 observed and expected deep root proportions (R^2=0.57, $P<0.0001$, n=137), we focused on deep

200 root proportions in multiple regression analyses of aboveground biomass. These analyses show

201 that deep root proportion explains variance in aboveground biomass that is not accounted for by

202 planted species richness, legume presence, legume abundance, or various parameters related to N

203 availability, including root N content, total soil N, extractable soil nitrate, and the rate of net N

204 mineralization (Table 1). This apparent effect of deep root proportion on aboveground biomass is

205 not simply a result of the correlation between deep root proportion and total root biomass, since

206 both deep root proportion and total root biomass were significant predictors of aboveground

207 biomass when included in multiple regression models ($P<0.05$, regardless of whether other

208 predictors discussed above were included or excluded). When compared to the N-related

209 parameters, deep root proportion explained as much or more variance in aboveground biomass,

210 according to sums-of-squares, and had an effect size that was as large or larger, according to *t*

211 values and standardized model coefficients (Bring 1994) (Table 1). Results were similar for

212 regression models of total root biomass that used the difference between observed and expected

213 deep root proportions as a predictor instead of the observed deep root proportion; deviations

214 from expected deep root proportions explained variation in root biomass that was not accounted

215 for by species richness, legume presence or abundance, or N-related parameters (not shown).

216

217 **Discussion**

218   In this experiment, the most diverse and productive plant communities also had the

219 deepest distributions of root biomass (Fig. 1A-C, E-G). The relationship between diversity and

220 deep root proportion arose, not because diverse plant communities contained a higher proportion

221 of deep-rooted species, but because of *plasticity* in root biomass allocation in diverse

222 communities. This conclusion is supported by trends in the difference between observed and

223 expected root depth distributions (Fig. 1D,H). In plant communities with less than 8 species,

224 observed deep root proportions were similar to expected values based on the relative abundance

225 of species and the rooting characteristics of those species in monoculture (i.e. root depth

226 distributions and root:shoot ratios). However, communities with 8 or more plant species had

227 higher deep root proportions than expected, reflecting the *net* effect of adjustments to rooting

228 depth and/or root:shoot ratios by one or more plant species. Furthermore, the covariance of root

229 depth distributions and plant biomass, both above and belowground, depended not only on plant

230 species richness, but also on the presence of different plant functional groups (Fig. 1E-H).

231   Collectively, our results suggest that diversity-dependent shifts in rooting depth, which

232   were enhanced by plasticity in root allocation, contribute to the positive diversity-productivity

233   relationship in this experimental grassland. We hypothesize that deeper root distributions (at the

234   community level) enhanced plant productivity by enabling three related attributes of plant

235   communities to increase, including: i) spatial complementarity among species, ii) biomass of

236   absorptive roots, and iii) uptake of limiting resources in soils. To test this hypothesis requires

237   data on the distribution of root biomass *for each species* in a community (e.g. Mommer et al.

238   2010) and uptake of resources from different soil depths (e.g. Kulmatiski and Beard 2012).

239   Notably, even after we accounted for root depth distributions and other factors underlying

240   the diversity-productivity relationship at our site, such as legume presence and N availability

241   (Fornara and Tilman, 2009), species richness explained additional variance in aboveground

242   productivity. Therefore, other, unidentified factors likely contributed to the higher productivity

243   of diverse plots, such as the amelioration of pathogen effects (Maron et al. 2011, Schnitzer et al.

244   2011, de Kroon et al. 2012) or phenological complementarity (Fargione and Tilman 2005a).

245   *Why do more diverse communities have deeper root distributions?* The presence of

246   legumes was strongly associated with deep root depth distributions, but several lines of evidence

247   suggest the positive effects of species richness on the deep root proportion were not simply due

248   to the presence or dominance of deep-rooting legumes in diverse plots. First, species richness

249   still explained variation in root depth distributions after accounting for legume presence or

250   abundance (Table A2). Second, root depth distributions of the most diverse plots were deeper

251   than expected according to species' abundance and monoculture traits (Fig. 1D,H). Finally, for

252   plots planted with 16 species, the plots with the lowest abundance of legumes (aboveground) had

253   the deepest root depth distributions and the most apparent plasticity in root allocation (Fig. A2).

254   Below, we discuss how interspecific interactions and the presence of particular species might

255   explain the residual effects of species richness on root depth distributions (i.e. the effects of

256   species richness that cannot be explained by the presence or abundance of legumes).

257   *What caused root allocation to be more plastic in diverse plots?* Only communities with

258   both legumes and C4 grasses consistently had deeper root depth distributions than expected

259   according to monoculture traits (Fig. 1H); these communities also had the most root biomass

260   (Fig. 1F). One possible explanation for this apparent plasticity in root allocation is that C4

261   grasses might grow and maintain more deep roots if legumes increased N availability in deep

262   soils, through both N-fixation and mineralization of N in dead, N-rich legume roots. Earlier

263   studies documented that plant productivity in this experiment increased when both legumes and

264   C4 grasses were present, but explanations of this interaction focused on the complementarity of

265   relatively fixed, inherent traits. For example, compared to C3 grasses and forbs, the extensive

266   root systems and low N tissues of C4 grasses probably allow greater uptake of legume-derived N

267   and more efficient conversion of this N into biomass (HilleRisLambers et al. 2004, Fargione and

268   Tilman 2005b, Fargione and Tilman 2006, Fargione et al. 2007, Fornara and Tilman 2008). In

269   this study, we show that plasticity of root allocation could, through unknown mechanisms, also

270   contribute to the effect of legumes and C4 grasses on plant biomass, particularly belowground.

271   *Effects of individual species.* When using the presence or abundance of plant functional

272   groups as predictors of plant biomass, some of the variance in biomass that is attributed to

273   species richness could be accounted for by strong impacts of individual species within functional

274   groups. In our study, *Lupinus perennis* had the highest relative abundance of the legumes, the

275   largest effect of any species on the deep root proportion, and a large effect on plasticity in root

276   allocation. This is likely attributable not only to the abundance of *Lupinus perennis*, but also to

277   its possession of one or more unique traits relative to other legumes. For example, *Lupinus*

278   *perennis* is the only legume species that actively grows in early spring. Since *Lupinus perennis*

279   was planted in nearly all of the most diverse plots (33 of 35 plots), its presence likely contributed

280   to the effects of planted species richness on the deep root proportion.

281   The presence of the C4 grass *Schizachyrium scoparium* in multispecies communities was

282   also associated with deeper than expected root biomass distributions. *Schizachyrium scoparium*

283   is a shallow rooting species in monoculture (Table A3) with a strong ability to reduce shallow

284   soil nutrient concentrations (Fargione and Tilman 2005a), two characteristics that might induce

285   co-occurring species to shift allocation of root biomass to deeper soil horizons.

286   *How do our results relate to theory and results from other studies?* Investment in deep

287   roots is expected to be more advantageous when shallow soil horizons reach low levels of

288   nutrient or water availability as compared to deep soil horizons (Schenk 2008, Mommer et al.

289   2010, Skinner and Comas 2010). Alternatively, some species might root more deeply in response

290   to changes in the presence or density of roots from conspecifics or other plant species (Schenk

291   2006, Mommer et al. 2010), regardless of nutrient gradients (de Kroon et al. 2012). More data on

292   species-level rooting patterns, nutrient gradients, and nutrient uptake from different depths is

293   required to distinguish among these different possibilities. The limited data we have suggests a

294   potential role for nutrient gradients; nitrate concentrations in upper soil horizons were negatively

295   correlated with species richness ($P<0.0001$, $R^2=0.17$, using nitrate concentrations sampled in

296   mid-August 2006; see also Fargione and Tilman (2005b) and soil moisture in the upper 20 cm of

297   soil was depleted by the presence of legumes (not shown; see also Fornara and Tilman 2009).

298   Earlier studies of pasture forage species, including legumes, also found that root depth

299   distributions were deeper and plant productivity was higher for more diverse plant mixtures

300   (Skinner et al. 2004, Skinner et al. 2006, Skinner and Comas 2010). Yet, because the most

301   diverse plots contained species that were not present in any replicate of lower diversity plots, the

302   apparent richness effect is difficult to evaluate (Sanderson et al. 2004). Other field and laboratory

303   experiments have observed that the depth distribution of root biomass did *not* increase with plant

304   species richness (Bessler et al. 2009, Wacker et al. 2009, Mommer et al. 2010). There are several

305   reasons that could explain the contrasting results of these studies: i) the absence of legumes

306   (Mommer et al, 2010) or the low levels of species richness (≤ 6 species; Wacker et al. 2009;

307   Mommer et al. 2010) in some studies, ii) use of soils that are more nutrient rich than our study

308   site (Bessler et al. 2009), fertilized soils (Wacker et al. 2009), or soils that do not have realistic

309   vertical resource gradients (Mommer et al. 2010), and iii) differences among studies with respect

310   to how species richness and functional composition influence soil resource gradients. For

311   example, at an experiment in Jena, Germany that has a comparable design to our experiment, N

312   availability in soil is generally higher and diverse plots did not reduce nitrate concentrations in

313   soil after the first year (Oelmann et al. 2011); thus, increases in aboveground biomass with

314   species richness might be supported without additional investment in root biomass, evident in

315   reduced root to shoot biomass ratios (Bessler et al. 2009).

316   *Conclusions.* In this 12-year-long experiment, the most productive and diverse plant

317   communities had the deepest distributions of root biomass, partly as a consequence of plasticity

318   in root allocation that arose when both legumes and C4 grasses were present. Future studies

319   should address the role of root depth distribution and belowground plasticity in other grassland

320   diversity experiments. Additional research is also needed to evaluate whether spatial

321   complementarity and uptake of soil resources were enhanced in diverse plots by root plasticity.

322

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408

409 **APPENDIX A**

410 Tables report the deep root proportion of monocultures and results of statistical models of root

411 biomass, deep root proportions, and differences between observed and expected deep root

412 proportions. Figures show root biomass for each depth increment and species richness (Fig. A1)

413 and correlations of the deep root proportion and the difference between observed and expected

414 deep root proportion with the abundance of legumes and C4 grasses in diverse plots (Fig. A2).

415 **Tables**

416 **Table 1**. Multiple regression and ANCOVA models of aboveground biomass. *P* values less than 0.001 are in bold, between 0.001 and

417 0.01 are in bold italic, between 0.01 and 0.05 are in italic, and between 0.05 and 0.1 in normal print.

Factor	*N parameters only*			*N parameters & % deep roots*			*N par., leg. pres., & no. of species*			*all predictors*		
	% *SS*[*]	*t* value	Effect size[#]	% *SS*[*]	*t* value	Effect size[#]	% *SS*[*]	*t* value	Effect size[#]	% *SS*[*]	*t* value	Effect size[#]
initial soil N%	1	1.9	22	*1*	*2.0*	*21*	*2*	*3.2*	*28*	*2*	*3.1*	*27*
Δ soil N%[†]	**6**	**4.1**	**45**	**5**	**3.8**	**39**	*2*	*3.3*	*29*	*2*	*3.3*	*28*
Δ root N%[‡]	**5**	**3.6**	**44**	*3*	*3.2*	*36*	ns	ns	ns	ns	ns	ns
net N mineralization	**11**	**5.3**	**73**	**4**	**3.8**	**49**	*2*	*3.0*	*34*	1	2.5	28
soil NO$_3$[¶]	**13**	**-5.8**	**-78**	**9**	**-5.5**	**-67**	*2*	*-3.2*	*-38*	*2*	*-3.1*	*-35*
% deep roots	na	na	na	**11**	**6.0**	**69**	na	na	na	*2*	*3.3*	*35*
no. of species	na	na	na	na	na	na	**6**	**5.3**	**65**	**6**	**5.2**	**62**
Legume presence[§]	na	na	na	na	na	na	**9**	**6.2**	**75**	**5**	**4.8**	**59**
R^2		0.44			0.55			0.68			0.70	
n		152			152			152			152	

418 [*]The percent of total sums-of-squares (SS) for aboveground biomass that can be uniquely attributed to each predictor variable, using Type III sums-of-squares.

419 [#]Effect size was estimated by multiplying the model coefficient by two standard deviations of the predictor (similar to Bring, 1994). The effect size is the amount

420 of aboveground biomass (g per m^2) predicted to be gained or lost when each predictor shifts from one SD below the mean to one SD above the mean. [†]The

421 increase in soil N% between 1994 and 2006. [‡]The increase in root N% between 1995 and 2006. [¶]Soil nitrate concentrations. For details on N-related parameters,

422 see Fornara and Tilman (2009). [§]Similar results were observed when using legume abundance. na = not included in the model. ns = not significant (*P*>0.1).

423 **Figure legends**

424 **Figure 1**. Effects of species richness and community composition on plant biomass, the deep

425 root proportion, and the difference between observed and expected deep root proportions. The

426 categories describing community composition were chosen based on results of statistical models

427 of the deep root proportion and the difference between observed and expected deep root

428 proportions (Tables A2 and A4). Error bars indicate standard error. Within each panel, bars

429 labeled with different letters are significantly different according to Tukey tests ($P<0.05$).

430