1 **Interactions among resource partitioning, sampling effect, and facilitation**

2 **on the biodiversity effect: A modeling approach**

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21

22   **Abstract**

23   Resource partitioning, facilitation, and sampling effect are the three mechanisms

24   behind the biodiversity effect, which is depicted usually as the effect of plant-species

25   richness on aboveground net primary production. These mechanisms operate

26   simultaneously but their relative importance and interactions are difficult to unravel

27   experimentally. Thus, niche differentiation and facilitation have been lumped together

28   and separated from the sampling effect. Here, we propose three hypotheses about

29   interactions among the three mechanisms and test them using a simulation model. The

30   model simulated water movement through soil and vegetation, and net primary

31   production mimicking the Patagonian steppe. Using the model, we created grass and

32   shrub monocultures and mixtures, controlled root overlap and grass water-use efficiency

33   (WUE) to simulate gradients of biodiversity, resource partitioning and facilitation. The

34   presence of shrubs facilitated grass growth by increasing its WUE and in turn increased

35   the sampling effect whereas root overlap (resource partitioning) had, on average, no

36   effect on sampling effect. Interestingly, resource partitioning and facilitation interacted so

37   the effect of facilitation on sampling effect decreased as resource partitioning increased.

38   Sampling effect was enhanced by the difference between the two functional groups in

39   their efficiency in using resources. Morphological and physiological differences make

40   one group outperform the other, once those differences were established further

41   differences did not enhance the sampling effect. In addition, grass WUE and root overlap

42   positively influence the biodiversity effect but showed no interactions.

43

44   **Keywords**

45   1. resource partitioning

46   2. facilitation

47   3. sampling effect

48   4. Patagonian steppe

49   5. biodiversity and ecosystem functioning

Introduction

51   Understanding the relationship between biodiversity and ecosystem functioning is crucial

52   to assess some of the consequences of species loss (Chapin et al. 2000). In this field, a

53   central hypothesis is that the rate of ecosystem processes increases with biodiversity

54   (Vitousek and Hooper 1993; Schläpfer and Schmid 1999). To test this hypothesis,

55   manipulative experiments created monocultures and species mixtures representing the

56   low and high end of biodiversity gradients, and estimated aboveground net primary

57   production (ANPP), an integrative variable representing ecosystem processes. These

58   studies found, in general, a positive relationship between plant-species richness and

59   ANPP (Tilman et al. 1996; Hector et al. 1999; Flombaum and Sala 2008) , which is

60   accounted for by three different mechanisms: resource partitioning, facilitation among

61   species (together known as niche complementarity), and sampling effect (Huston 1997;

62   Tilman 1997; Loreau 2000; Loreau and Hector 2001; Mulder et al. 2001; Flombaum and

63   Sala 2012). Resource partitioning is the use of different resources by different species as

64   a result of evolutionary niche separation. In high diversity ecosystems, fine resource

65   partitioning results in high ANPP because more species means that more traits are

66   expressed that can therefore exploit resources more thoroughly (Tilman et al. 1997).

67   Facilitation, here used as a synonymous with positive interactions, represents benefits

68   provided by one species that can increase the effective niche of other species by habitat

69   amelioration, enhanced recruitment or predation refuge; and consequently results in

70   higher ANPP (Bruno et al. 2003). The sampling effect in biodiversity and ecosystem-

71   functioning experiments is associated with the chance of including the most productive

72   species in a randomly assembled mixture (Huston 1997; Tilman 1997). The sampling

73   effect is based on the idea that in a community there are always a few species that

74   outperform the others. Therefore, ANPP increases with species richness just because of

75   the higher probability of including outperforming species in the mixture.

76   The individual effects of resource partitioning, facilitation and sampling effect are

77   well established; on the contrary the interactions among the three of them are uncertain.

78   Especially, the effects of resource partitioning and facilitation on the sampling effect are

79   poorly understood. *Hypothesis 1*: resource partitioning positively affects sampling effect

80   because, under conditions of low resource partitioning, it would be difficult for a single

81   species to outperform all others. For the sampling effect to occur, a species needs to

82   outperform all others in the mix; and the probability of such species to exist increases as

83   differences among species increase. *Hypothesis 2*: facilitation positively affects the

84   magnitude of the sampling effect because the benefits from facilitation could be the

85   characteristic that determines one species outperforming others. Therefore, facilitation

86   increases the probability that a recipient of facilitation benefits sufficiently to outperform

87   all other species in the mix. *Hypothesis 3*: the interaction between resource partitioning

88   and facilitation has no influence on the sampling and biodiversity effects. Resource

89   partitioning and facilitation result from independent morphological and physiological

90   characteristics of individual species, hence their effect on the biodiversity effect in

91   independent.

92   Interactions among resource partitioning, sampling effect and facilitation would

93   be difficult to reveal using field experimentation because the number of experimental

94   units would be prohibitive and because of the difficulty disentangling effects of

95   facilitation and resource partitioning. Consequently, facilitation is commonly lumped

96 with resource partitioning and is differentiated from the sampling effect (Loreau and

97 Hector 2001; Mulder et al. 2001; Vanelslander et al. 2009; Crawford and Whitney 2010).

98 Here, we developed a simulation model of water movement and ANPP in an arid

99 ecosystem to test hypotheses 1 to 3. We modified plant-life-form richness, root

100 distribution, and water-use efficiency to generate three independent gradients of

101 biodiversity, resource partitioning, and facilitation. Specifically, we altered root overlap

102 between shrubs and grasses to represent different degrees of resource partitioning.

103 Increasing root overlap represents decreasing resource partitioning since both plant

104 functional types explore the same soil resources. We modified water-use efficiency

105 (WUE) of grasses in the presence of shrubs as a way of representing the physiological

106 outcome of the facilitation resulting from the protective effect of shrubs over grasses.

107 Increased grass WUE in the presence of shrubs represents high facilitation. Using the

108 simulation model, we estimated: (1) the biodiversity effect as the difference in modeled

109 and expected ANPP, and (2) the sampling effect using Loreau and Hector's method

110 (2001).

111 We focused on arid ecosystems because they are largely influenced by facilitation

112 and resource partitioning (Sala et al. 1989; Bertness and Callaway 1994; Bruno et al.

113 2003; Craine et al. 2003; Flombaum and Sala 2012) and because their low diversity

114 provides ideal models to study biodiversity and ecosystem functioning relationships

115 (Flombaum and Sala 2008). We parameterized our model to represent major ecological

116 variables in an arid ecosystem, the Patagonian steppe. We chose this particular site

117 because we had data from a manipulative experiment that assessed the effect of

118 biodiversity on ecosystem functioning (Flombaum and Sala 2008; Flombaum and Sala

119 2012) and reliable information on climate, ecosystem structure and functioning (Aguiar

120 and Sala 1994; Jobbágy and Sala 2000). For the sake of simplicity, we only considered

121 the main life forms of the Patagonian steppe, grasses and shrubs, that account for 95% of

122 ANPP (Jobbágy and Sala 2000), use different sources of water (Sala et al. 1989), and

123 establish facilitative interactions (Aguiar and Sala 1994).

124

125 **Methods**

126 *1. Model description*

127   We developed a model that simulates soil water movement and ANPP dynamics

128 in the Patagonian steppe with daily time step forced with precipitation and temperature

129 records. The model source code was written in Object Pascal using IDE Lazarus v1.0

130 (www.lazarus.freepascal.org). In the model, water entered the system as rainfall, moved

131 downward through three soil layers, and exited the system as soil evaporation, plant

132 transpiration, and deep percolation (Fig. 1A). Evaporation only occurred from the top

133 layer where no root was present. Plants uptake water from the lower two soil layers and

134 their water-use efficiency linked transpiration to biomass production (Fig. 1A). A full

135 description of the model equations is available in Supplemental Information 1.

136 *2. Simulations*

137 We simulated gradients of biodiversity, grass water-use efficiency in the presence of

138 shrubs and root-overlap between grasses and shrubs (Figs. 1B, C and D). The model

139 observed output was biomass production by grasses and shrubs. We estimated the

140 biodiversity effect as the difference between the ANPP of the grass-shrub mix and the

141 ANPP predicted based on the productivity of the grass or shrub monocultures. Then, we

142   split the biodiversity effect into the sampling effect using Loreau and Hector's additive

143   partitioning scheme (2001).

144   *Parameter adjustment*

145   We tuned parameters (ε, WUE, γ, δ, *sat*, *wil*, *Ts*, α_{ev}, and α_{per}, Table 1) to

146   reproduce ANPP and ecosystem water-use efficiency for the Patagonian Steppe. We set

147   saturation and wilting point parameters (*sat* and *wil*) with standard values for sandy soils;

148   and the ratio between aboveground and belowground biomass (γ), and the depth of the

149   three soil layers (L_5, L_{35}, and L_{100}) with typical values for the Patagonian Steppe (Table

150   1). The other parameter values were set arbitrarily and adjusted in successive iterations to

151   improve the fit. For the calibration, shrub roots were restricted to the bottom layer, and

152   grass roots to the middle layer (Table 1), representing a case of zero root overlap.

153   Our model reproduced long term averages for the Patagonian Steppe. We

154   simulated grass and shrub ANPP using 19 years of climatic data, and compared them

155   with 15 and 19 years of grass and shrub field observations of ANPP (Jobbágy and Sala

156   2000; Flombaum and Sala 2009). Our model simulated a 3.5 and 2.5% higher than

157   observed mean total ANPP and mean rain-use efficiency respectively (Table 2); ANPP

158   for grasses and shrubs was 1.1 and 2.0 g m^{-2} yr^{-1} higher; however none of these mean

159   values were statistically different ($p>0.05$; Table 2). Also, the model reproduced the

160   observed relationship between mean annual precipitation and ANPP for grasses, shrubs,

161   and both combined (Fig. 2). Finally, we performed a sensitivity analysis in which we

162   modified each of the parameters by $\pm$ 10% and estimated the percent of change in mean

163   ANPP using 19 years of climatic data. No parameter significantly changed the mean

164   ANPP (*t*-test; $P>0.05$). The parameters of water-use efficiency for shrubs and grasses

165 (WUE$_{SH}$ and WUE$_{GR}$), and the saturation point of the middle layer (sat_{L100}) had the

166 largest impact on ANPP. ANPP increased by 5.5, 5.2 and 5.5 % with a 10% increase in

167 WUE$_{SH}$, WUE$_{GR}$ and sat_{L100} respectively (Table 1: values in parenthesis).

168   The focus of this exercise was not to reproduce the Patagonian steppe functioning

169 from first principles but rather to mimic its dynamics to evaluate the effects of root

170 overlap and grass water-use efficiency on the biodiversity and sampling effect. Based on

171 the modeled and observed mean values for the Patagonian Steppe (Table 2), the

172 relationship between the sensitivity of the parameters (Table 1) and the relationship

173 between ANPP and precipitation (Fig. 2), we found that our model was well suited to

174 reproduce major patterns of the Patagonian steppe.

175 *Biodiversity gradient*

176   We simulated a gradient of life-form richness with grass and shrub growing as

177 monocultures or together as a mixture (Fig. 1b). Monocultures and mixtures started with

178 the same initial biomass, reproducing the design of a replacement-series experiment. We

179 estimated ANPP for three consecutive years (1986 to 1988), with each growing season

180 starting at the end of autumn. We initialized the mixture at 50% grasses and 50% shrubs

181 in the first year, and set the proportions at the beginning of subsequent years according to

182 the productivity of the life form in the preceding year. Life-form proportions were used to

183 estimate the biodiversity and the sampling effects (Supplemental Information 2.1).

184 *Resource partitioning gradient*

185   We simulated a gradient of root overlap to represent resource partitioning. We

186 modified grass and shrub root distributions in the middle and bottom soil layers (Fig. 1c)

187 (Supplemental Information 2.2). The root overlap gradient had a value of zero when

188   grasses had their roots in the middle layer and shrubs in the bottom layer ($root_{GR\text{-}L35} = 1$;

189    $root_{GR\text{-}L100} = 0$; $root_{SH\text{-}L35} = 0$; $root_{SH\text{-}L100} = 1$), and a value of one when grasses and shrubs

190   have exactly the same root distribution with half of their roots in each layer ($root_{SH\text{-}L100} =$

191    $root_{GR\text{-}L100} = root_{SH\text{-}L35} = root_{GR\text{-}L35} = 0.5$).

192   *Facilitation gradient*

193   Facilitation was defined as the amelioration on physical conditions for grasses by

194   the presence of shrubs. We represented facilitation as an increase in grass WUE when

195   grasses occur in the mix with shrubs (Fig. 1d), reproducing an effect observed in arid

196   ecosystems (Bertness and Callaway 1994; Armas and Pugnaire 2005). We changed the

197   grass WUE parameter to create the gradient. WUE for grasses growing in monoculture

198   was 0.65 g m^{-2} mm H$_2$O^{-1}, and grass WUE increased in steps of 0.05 g m^{-2} mm H$_2$O^{-1} up

199   to 0.95 g m^{-2} mm H$_2$O^{-1} in the mix. The minimum value of facilitation, 0.65 g m^{-2} mm

200   H$_2$O^{-1}, resulted from parameter tuning to reproduce mean values in the Patagonian Steppe

201   (Section 1.1 and Table 1). We arbitrarily set the maximum WUE at 0.95 g m^{-2} mm H$_2$O^{-1}.

202   Finally, we rescaled the gradient from zero to one, to compare with the resource

203   partitioning gradient.

204   *3. Data analysis*

205   We performed a multiple regression analysis with biodiversity effect or sampling

206   effect as response variables, and root overlap, increased grass WUE, and their interaction

207   as predictors using MATLAB (Mathworks, MA). The use of a zero to one scale for root

208   overlap and grass WUE allowed to compare the relative effects of each predictive

209   variable. We reported regression parameters as significant if their 95% confidence

210   interval did not include zero.

Results

211

212   The sampling effect expressed as a fraction of ANPP, was on average unrelated to

213   root overlap (RO), which simulated resource partitioning. The sampling effect increased

214   with increased grass WUE, which simulated facilitation (Fig. 3a, Table 3). Most

215   interesting is that there was a significant interaction RO- WUE so as facilitation increased

216   the effect of resource partitioning on sampling effect decreased. When there is no

217   facilitation of shrubs on grasses, resource partitioning increased sampling effect. On the

218   contrary, when facilitation is maximal, resource partitioning decreased the sampling

219   effect.

220   The biodiversity effect, which was expressed relative to ANPP, increased with

221   root overlap and grass WUE, which simulated gradients of resource partitioning and

222   facilitation respectively (Fig. 3b). The biodiversity effect reached its highest value when

223   root overlap was minimal and grass WUE was maximal. Changes in root overlap had

224   larger effects than grass WUE. The biodiversity effect increased seven times between 1

225   and 0 root overlap (i.e. low and high resource partitioning) at 0 increased in grass WUE

226   (Fig. 3b: dotted line,). Also, the biodiversity effect increased five times between the 0 and

227   1 grass WUE at 1 root overlap (i.e. no resource partitioning) (Fig. 3b: circle vs. largest

228   triangle). In addition, the multiple regression slope of root overlap was 2.7 times higher

229   than that of grass WUE (Table 3). Finally, we observed no interaction between root

230   overlap and grass WUE on the biodiversity effect (Table 3).

Discussion

232   Our results indicated that, on average, root overlap (simulating resource

233   partitioning) did not affect sampling effect but grass WUE (simulating facilitation) did.

234   Most interesting is the interactive effect of resource partitioning and facilitation on the

235   sampling effect. As facilitation increased, the effect of resource partitioning on sampling

236   effect decreased. These results suggest that the magnitude of the sampling effect depends

237   on the functional differences among functional groups (or species) that make one group

238   outperform the other. Differences between shrubs and grasses in our experiment result

239   from either facilitation or resource partitioning, which compensate for each other. When

240   both groups have the same root patterns the effects of differential WUE is responsible for

241   the sampling effect. On the contrary, when there is no facilitation root depth is the

242   variable that determines that one species outperforms the other and determines the

243   magnitude of the sampling effect.

244   Both facilitation and resource partitioning positively affected the biodiversity

245   effect (Fig. 3B) but there was no interaction among them supporting hypothesis 3. Root

246   overlap and grass WUE affect the ability of the community to utilize resources and

247   therefore affect the biodiversity effect but they are not related to each other. Decreased

248   root overlap increases water capture and increase WUE increases efficiency by reducing

249   transpiration per unit of production.

250   Resource partitioning and facilitation (Loreau and Hector 2001), directly

251   influenced the biodiversity effect in agreement with empirical results (Mulder et al. 2001;

252   Flombaum and Sala 2012). In addition, facilitation and its interaction with resource

253   partitioning indirectly influenced the biodiversity effect through the sampling effect (Fig.

254   4). In our simulation experiment, the sampling effect was a minor fraction of the

255   biodiversity effect (Fig. 3) similar to what was observed for the Patagonian Steppe

256   (Flombaum and Sala 2008).

257 Our modeling experiments provided a possible explanation for results of

258 biodiversity and ecosystem functioning experiments performed with seeded ecosystems.

259 Experiments showed that the biodiversity effect increased with time mostly because of an

260 increase in niche complementarity, and at the same time they showed an accompanying

261 reduction in the sampling effect (van Ruijven and Berendse 2005; Fargione et al. 2007).

262 Resource partitioning gradients, like the one described here, could occur through time

263 from early to late successional stages in sowed experiments as phenotypic characteristics

264 get fully expressed through time (Sala 2001), so our decreasing root overlap could be

265 replaced by time in seeded experiments. Our simulations suggested that facilitation and

266 resource partitioning were the major mechanisms of the biodiversity effect, although in

267 early successional stages (i.e. low resource partitioning) their effect occurred indirectly

268 through the sampling effect (Figs. 3 and 4).

269 The simulated facilitation-partitioning interaction resulted from the asymmetry of

270 the relationship between grasses and shrubs. Grasses were benefited by shrubs by reduced

271 evaporative demand resulting in higher water-use efficiency. Simultaneously, the

272 increased grass growth and transpiration reduced the amount of water that reaches the

273 lower soil layers. Consequently, under conditions of high resource partitioning and when

274 shrubs absorb water only from lower layers, the facilitation effect on grasses produced a

275 negative effect on shrub water availability and growth. There is empirical evidence of a

276 facilitation shifting to inhibition depending on the life stage, physiology and environment

277 (Callaway and Walker 1997; Graff et al. 2007). The pattern simulated here, in which the

278 species that receives the benefit negatively impacts the species that provides the benefit,

279 has also been observed in grass and legume ecosystem (Temperton et al. 2007; Marty et

280 al. 2009).

281   Disentangling the relative importance and interactions of the three mechanisms of

282 the effect of biodiversity on ecosystem functioning is important from the basic

283 understanding of the relationships between community structure and ecosystem

284 functioning and from the conservation point of view. Our manipulation of grass water-use

285 efficiency and root overlap representing gradients of facilitation and resource partitioning

286 in a modeling experiment adds a complementary perspective to previous work that

287 manipulated resource partitioning, competitive interactions or both (Yachi and Loreau

288 2007; Carroll et al. 2011; Verón et al. 2011; Loreau et al. 2012). Field experiments that

289 specifically addressed facilitation and resource partitioning on biodiversity and ecosystem

290 functioning experiments found little or no influence of facilitation (Gross et al. 2007;

291 Northfield et al. 2010), which highly contrast with our modeling perspective. As a whole,

292 our modeling results show a much larger effect of facilitation and resource partitioning

293 than the sampling effect, highlighting the need for conserving biodiversity for the

294 maintenance of ecosystem services.

295

307

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390

391

FIGURES and TABLES

394

395 **Table 1: Model parameters and their influence on mean ANPP.** Values for each

396 parameter were set to represent mean ANPP and rain use efficiency for the Patagonian

397 steppe. In brackets, percent change in mean ANPP with a 10% increase in the parameter

398 indicating the sensitivity of the model. Definitions: ε senescent biomass constant, WUE

399 water-use efficiency; γ ratio between above and belowground biomass; δ water

400 absorption rate; *root* proportion of root in a layer; t*B* aboveground green biomass; *sat* and

401 *wil* water retention constant for saturation and wilting point; *h* height of the soil layer; *Ts*

402 temperature constant; α_{ev} and α_{per} water conductance constant for evaporation and

403 percolation; *L5*, *L35*, and *L100* for top, mid, and bottom soil layer. Superscripts [a, b] and [c]

404 denote values that changed in the experiments where we modified grass WUE to

405 represent changes in facilitation and where we changed root overlap to represent changes

406 in resource partitioning.

407

Parameter (units)	Grasses	Shrubs	*L5*	*L35*	*L100*	Other
ε (day^{-1})	0.01(-0.8)	0.15(0.0)				
WUE (g m^{-2} mm H$_2$O^{-1})	0.65(5.5)[a]	0.65(5.2)				
γ (none)	1:1.75(0.9)	1:3(1.5)				
δ (mm H$_2$O day^{-1} g^{-1} m^{-2})	0.02(0.9)	0.02(0.3)				
root$_{f\text{-}L35}$[b]	1	0				
root$_{f\text{-}L100}$[b]	0	1				
B (g m^{-2})	30[c]	30[c]				
sat (mm H$_2$O cm^{-1})			1(-4.4)	1(1.9)	1(5.5)	
wil (mm H$_2$O cm^{-1})			0.5(2.4)	0.5(-1.0)	0.5(-3.1)	
h (cm)			5(-2.3)	30(0.8)	65(2.7)	
Ts (°C)						4(-0.4)
α_{ev} (day^{-1})						0.1(-1.1)
α_{per} (day^{-1})						1(0.2)

410

411 **Table 2: Modeled and observed mean ANPP and rain use efficiency for the**

412 **Patagonian steppe.** We modeled ANPP using 19 years of climatic data (i.e. temperature

413 and precipitation) for Rio Mayo field station, Chubut, Argentina. Observed field

414 estimations of ANPP were obtained from the same locality, and mean values are based on

415 15 and 19 years of samples for shrubs and grasses respectively (Jobbágy and Sala 2000;

416 Flombaum and Sala 2009). References: ANPP aboveground net primary production;

417 RUE rain-use efficiency. Simulated mean ± 1SD values were obtained based on 19 years

418 of climatic data; observed mean ± 1SD values represent the mean of 15 and 19 years for

419 shrubs and grasses respectively. Values did not differ statistically ($p>0.05$).

420

	Modeled	Observed
ANPP total (g m^{-2} yr^{-1})	59.3 ± 20.8	56.3 ± 14.8
ANPP Grasses (g m^{-2} yr^{-1})	28.0 ± 9.4	26.9 ± 9.7
ANPP Shrubs (g m^{-2} yr^{-1})	31.3 ± 13.3	29.3 ± 9.0
RUE (g m^{-2} mm H$_2$0^{-1})	0.40 ± 0.14	0.39 ± 0.11

421

422

423

424 **Table 3: Root overlap (RO) and grass WUE influence on the sampling effect (SE)**

425 **and the biodiversity effect (BE).** Values represent the slopes ± 95% confidence interval

426 of a multiple linear regression. Values in bold did not include the zero within the 95%

427 confidence interval.

428

	SE	BE
Intercept	**-0.022 ± 0.004**	0.260 ± 0.026
RO	$3.2 \times 10^{-4} \pm 0.008$	**-0.265 ± 0.043**
grass WUE	**0.036 ± 0.008**	**0.102 ± 0.044**
RO ^{x} grass WUE	**0.032 ± 0.012**	0.064 ± 0.072
MS	0.005	0.120
F	251.9	167.9

429

430   **Figure 1: a) Model description and experiments of a) life-form richness, b) root**

431   **overlap, and c) increased grass WUE.** a) Model components, fluxes and controls. Solid

432   arrows and italics represent flows; dashed arrows controls; solid boxes state variables;

433   dotted box is illustrative to group soil components. Sub-indices: L5, L35, and L100 for

434   top, mid and bottom soil layer; SH and GR for shrubs and grasses; P water percolation;

435   W water content; U water uptake; W plant-water status; WUE water-use efficiency; B

436   plant biomass; ANPP aboveground net primary production. b) Simulated biodiversity

437   gradient with grass monoculture (left), shrub monoculture (middle), and mixture (right).

438   c) Simulated low, mid, and high root overlap representing a high mid and low resource

439   partitioning gradient (from left to right). The thickness of the arrow indicates the

440   proportion of root in each layer. d) Simulated increase in grass WUE representing a

441   facilitation gradient. From left to right: null, mid and high grass WUE; the thickness of

442   the arrow indicates the amount of facilitated WUE perceived by grasses in the presence

443   of shrubs.

444

445   **Figure 2: Relationship between the ANPP and mean annual precipitation (PPT) for**

446   **life forms combined, grasses, and shrubs.** Simulated ANPP was obtained using our

447   model and 19 years of climatic data. Observed ANPP was obtained from Jobbágy and

448   Sala (2000) and Flombaum and Sala (2009). Climatic and ANPP field observations were

449   obtained from the same locality in Rio Mayo field station, Chubut, Argentina.

450

451

452

453 **Figure 3: Influence of a) increased WUE for grasses and b) root overlap on the**

454 **sampling and the biodiversity effect.** Root overlap (RO) and increased grass WUE

455 simulated resource partitioning (RP) and facilitation (F) gradients. Lines in a) and b)

456 depict simulations with the same root overlap and same increased WUE for grasses. The

457 sampling and the biodiversity effect were expressed as a fraction of ANPP.

458

459 **Figure 4: Direct and indirect influences on the biodiversity effect.** The influences

460 identified in this figure result from an experiment using a simulation model that mimics

461 the Patagonian Steppe. The experiment was a full factorial design with root overlap and

462 grass WUE representing resource partitioning and facilitation. Facilitation and its

463 interaction with resource partitioning indirectly influenced the biodiversity effect through

464 the sampling effect.

465

466

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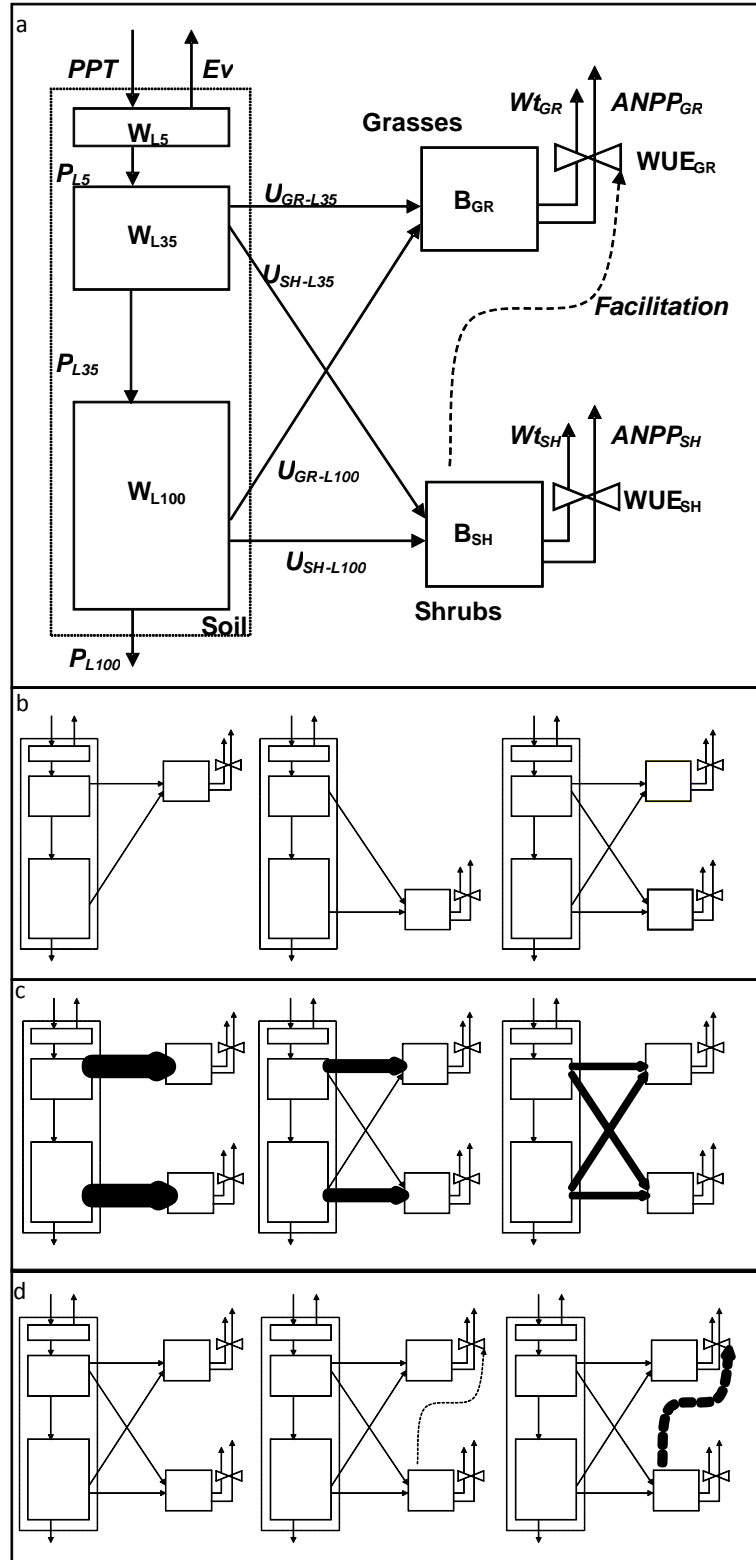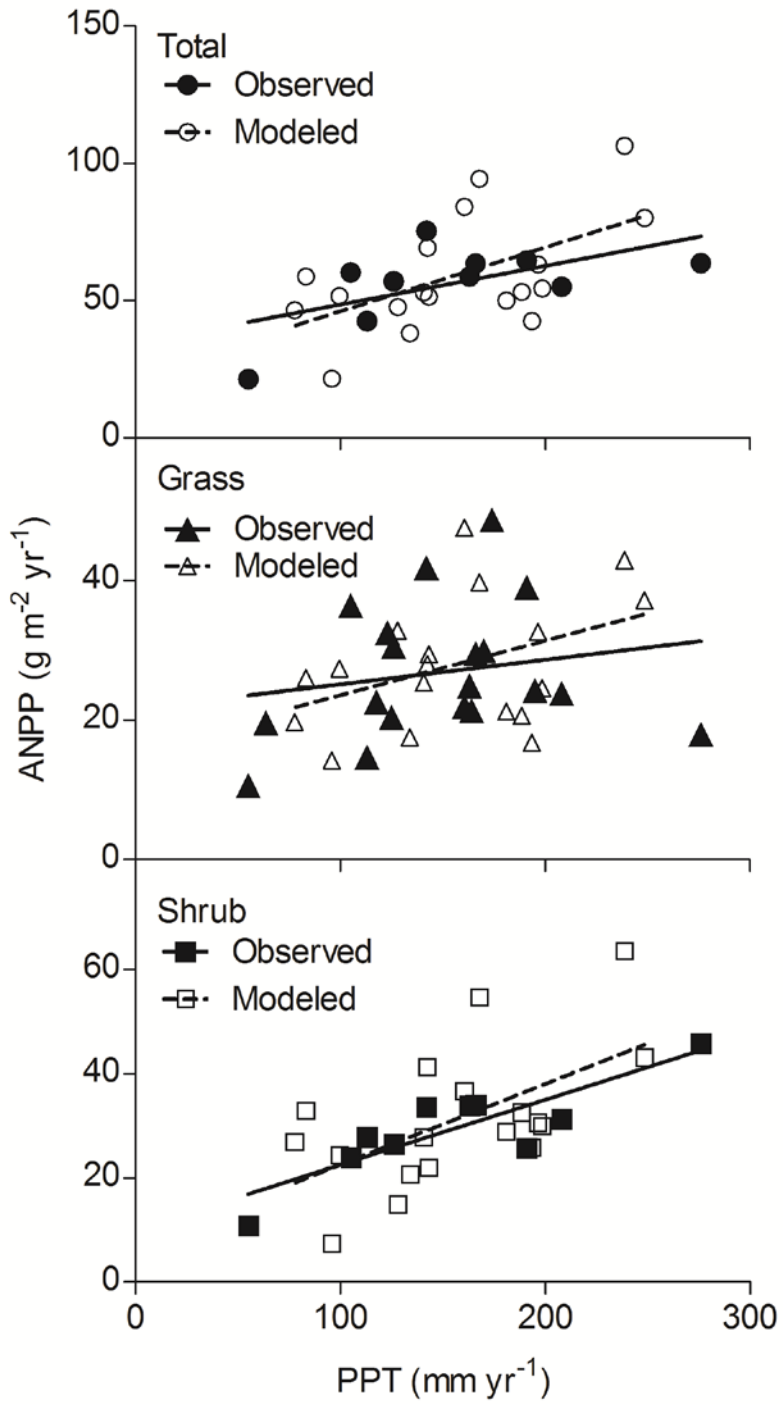470 Patagonian steppe. Ecological Applications 10:541-549
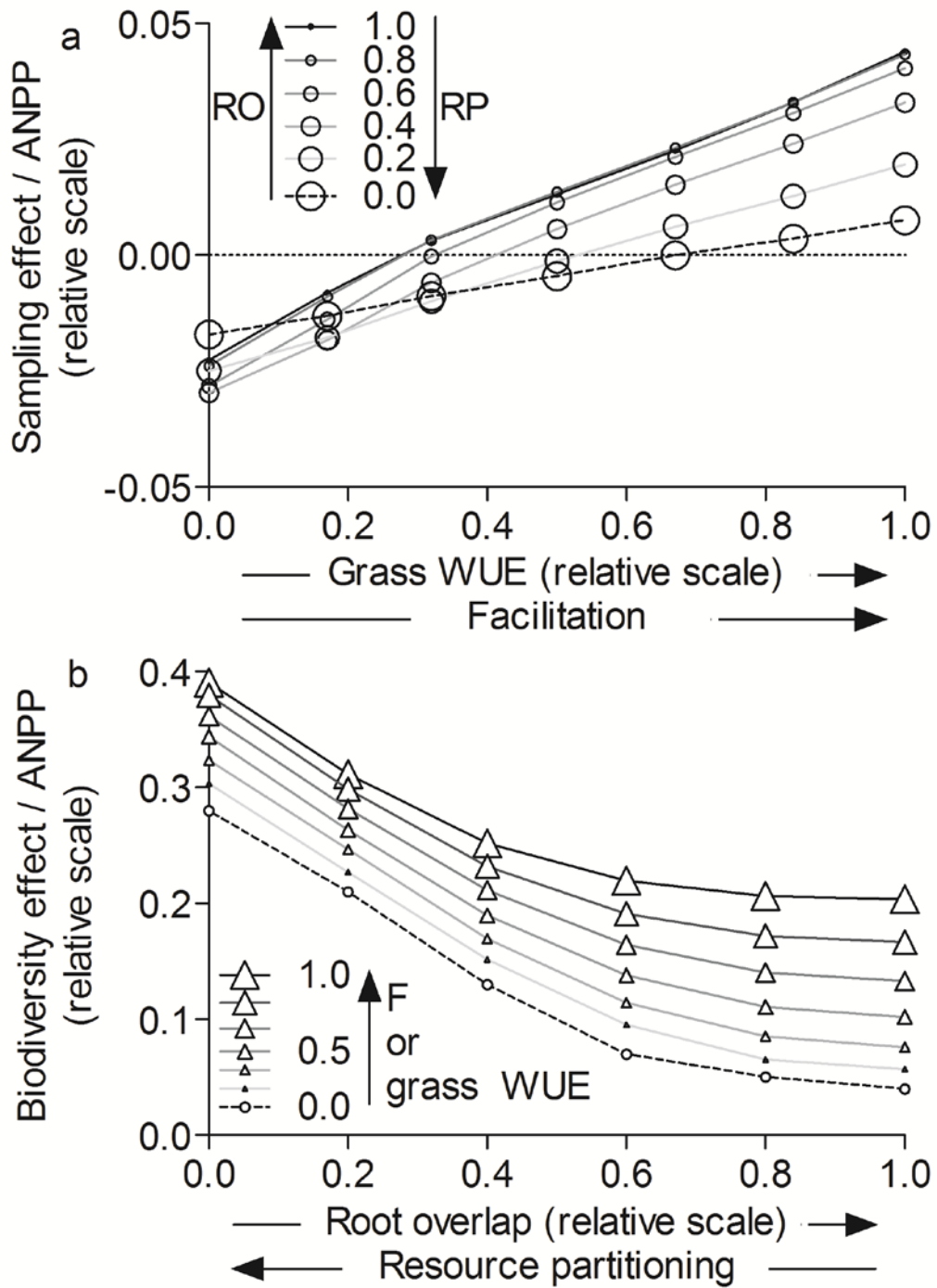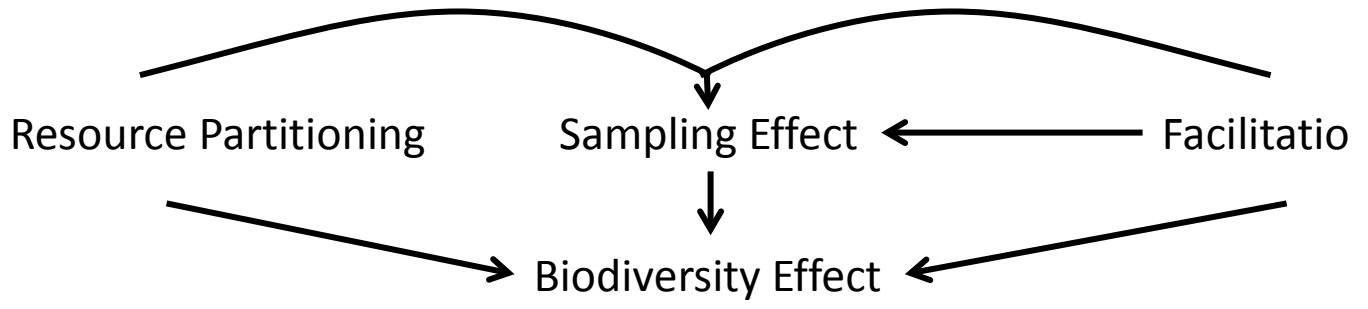
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FIGURE 1

FIGURE 2

FIGURE 3

FIGURE 4

Resource Partitioning   Sampling Effect   ←——— Facilitatio

Biodiversity Effect

473

474 **Interactions among resource partitioning, sampling effect, and**

475 **facilitation on the biodiversity effect: A modeling approach**

476
477 Pedro Flombaum, Osvaldo E. Sala & Edward B. Rastetter

SUPPLEMENTAL INFORMATION

478 *1. Model description*

479 *1.1. Components*

480 The components of our model are two life forms, grasses and shrubs, and three

481 soil layers. In the Patagonian steppe, grasses are shallow rooted and perennial, and shrubs

482 are deep rooted and deciduous. We divided one meter of soil depth into top, mid, and

483 bottom layers, with 0-5, 5-35, and 35-100 cm depth. Evaporation takes place from the top

484 layer (Paruelo et al. 1991), while the mid layer represents the layer with highest grass root

485 biomass (Soriano et al. 1987) and the bottom layer has the most shrub root biomass

486 (Fernandez and Paruelo 1988; Golluscio et al. 2006). Soil is coarse textured with high

487 proportion of sand and pebbles (Sala et al. 1989) that yields a low water-holding

488 capacity. Therefore, we used a soil-water-holding capacity of 1 mm H_2O cm soil^{-1} for the

489 entire soil profile. We calculated wilting (Ww_y, mm H_2O, eq. 1) and saturation (Ws_y, mm

490 H_2O, eq. 2) points for each y layer as

491 $$Ww_y = h_y \, wil_y \qquad \text{eq. 1}$$

492 $$Ws_y = h_y \, sat_y \qquad \text{eq. 2}$$

493 where h_y (cm) is the height of the y layer and wil_y (mm H_2O cm^{-1}) and sat_y (mm H_2O cm^{-}

494 ^{1}) are wilting and saturation constants. Water available in the y layer (Wa_y, mm H_2O) is

495 the difference between amount of water on y layer (W_y, mm H_2O) and Ww_y:

496 $$Wa_y = W_y\, Ww_y \qquad\qquad\qquad \text{eq. 3}$$

497 Wa_y is zero or positive.

498 *1.2. Water flow*

499 The water balance of the top layer (dW_{L5}/dt, mm H_2O day^{-1}, eq. 4) was simulated

500 by inputs in precipitation (PPT, mm H_2O day^{-1}) and outputs through evaporation (Ev, mm

501 H_2O day^{-1}, eq. 5) and percolation (P_{L5}, mm H_2O day^{-1}, eq. 8).

502 $$dW_{L5}/dt = PPT - Ev - P_{L5} \qquad\qquad \text{eq. 4}$$

503 Precipitation was the only water input into the system; we did not consider run-on nor

504 runoff because of the flat topography and coarse soil texture (Paruelo and Sala 1995).

505 Evaporation was the product between evaporation constant (α_{ev}, day^{-1}) and water

506 available in the top soil layer (Wa_{L5}).

507 $$Ev = \alpha_{ev}\, Wa_{L5} \qquad\qquad\qquad \text{eq. 5}$$

508 In the mid ($L35$) and bottom ($L100$) layers, the water balance (eqs. 6 and 7) was

509 simulated by inputs as percolation from the soil layer above (P_{L5}, or P_{L35}), and outputs as

510 percolation to the layer below (P_{L35}, or P_{L100}) and as uptake by shrubs and grasses ($U_{SH\text{-}y}$

511 $U_{GR\text{-}y}$, mm H_2O day^{-1}, eqs. 9 and 10).

512 $$dW_{L35}/dt = P_{L5} - P_{L35} - U_{SH\text{-}L35} - U_{GR\text{-}L35} \qquad \text{eq. 6}$$

513 $$dW_{L100}/dt = P_{L35} - P_{L100} - U_{SH\text{-}L100} - U_{GR\text{-}L100} \qquad \text{eq. 7}$$

514 The model simulates water movement (P_y, mm H_2O day^{-1}) by saturated flow and did not

515 represent unsaturated flow. Therefore, water moved downward but not upwards.

516 Unsaturated flow in this coarse-texture soil is very small and consequently not including

517 this flow should not result in a significant error (Paruelo and Sala 1995). Percolation (P_y,

518 eq. 8) from layer y was proportional (by constant α_{per}, day^{-1}) to the difference between

519　water in the layer (W_y) and the saturation point of the layer (Ws_y). P_y is either zero or

520　positive.

521　$$P_y = \alpha_{per} (W_y - Ws_y)$$　　　　　　eq. 8

522　　　　Plants transpired the same amount of water that they uptake (eqs. 9 and 10). We

523　simulated shrub water uptake from soil layer y ($U_{SH\text{-}y}$, mm H_2O day^{-1}) as an asymptotic

524　function of the water content of layer y using the following equation:

525　$$U_{SH-y} = \frac{Wa_y Br_{SH-y}\delta_{SH}}{Wa_y + (Ws_y - Ww_y)/2}$$　　　　eq. 9

526　$U_{SH\text{-}y}$ also increased with shrub-root biomass in layer y ($Br_{SH\text{-}y}$, g m^{-2}), and a constant

527　regulated absorption rate (δ_{SH}, mm H_2O day^{-1} g^{-1} m^2). In the denominator of eq. 9, a

528　constant number equivalent to 50% of potential water available [($Ws_y - Ww_y$)/2] and Wa_y,

529　gave the hyperbolic shape of the curve. Shrubs absorbed water from spring to early

530　autumn reproducing the phenology of green biomass in the Patagonian Steppe. We

531　simulated grass-water uptake ($U_{GR\text{-}y}$, mm H_2O day^{-1}) from soil layer y with a similar

532　equation but modified by a temperature factor (eq. 10).

533　$$U_{GR-y} = \left(\frac{Wa_y Br_{GR-y}\delta_{GR}}{Wa_y + (Ws_y - Ww_y)/2} \right)\left(\frac{(T - Ts)}{(T - Ts) + Tm} \right)$$　　　eq. 10

534　In the Patagonian Steppe, grass species are perennial and active all year around, but

535　winter activity is constrained by low temperatures. The temperature correction factor

536　reduced water uptake to 80% of the maximum capacity at 24 $^{\circ}$C, to 17% at 5°C, and to

537　0% below 4 $^{\circ}$C ($Ts = 4$ $^{\circ}$C, and $Tm = 5$ $^{\circ}$C). Root biomass of life form f in each layer y

538　($Br_{f\text{-}y}$, g m^{-2}) of eqs. 9 and 10, depended on the root to shoot ratio (γ_f, no units), the root

539　proportion in layer y ($root_{f\text{-}y}$, no units), and the plant aboveground biomass (B_f, g m^{-2}, eq.

540　11)

541 $$Br_{f\text{-}y} = root_{f\text{-}y}\, \gamma_f\, B_f \qquad\qquad\qquad\text{eq. 11}$$

542 Weather inputs were daily values of mean air temperature and precipitation, recorded

543 during 19 years at the experimental station INTA Río Mayo, (45° 41' S, 70° 16'W).

544 *1.3. Biomass production*

545 Daily changes in aboveground plant biomass (dB/dt, eq. 12) were simulated as the

546 difference between aboveground net primary production ($ANPP_f$, g m^{-2} day^{-1}, eq. 13) and

547 senescence (S_f, g m^{-2} day^{-1}, eq. 14) per life form f.

548 $$dB_f/dt = ANPP_f - S_f \qquad\qquad\qquad\text{eq. 12}$$

549 $ANPP_f$ increased with water use efficiency (WUE_f, g m^{-2} mm H$_2$O^{-1}) and the amount of

550 water transpired (Wt_f, mm H$_2$O day^{-1}, eq. 13)

551 $$ANPP_f = WUE_f\; Wt_f \qquad\qquad\qquad\text{eq. 13}$$

552 Wt_f equals the total water uptake by life form f (the sum of water uptake from mid and

553 bottom soil layers). Senescence of green biomass was seasonal; shrubs lost all their

554 aboveground green biomass at the end of the growing season (May), while grasses had a

555 progressive litter production until the start of the new season (end of September). For

556 both life forms, senescence was directly proportional to a constant ε_f (day^{-1}) and live

557 biomass (B_f, g m^{-2})

558 $$S_f = \varepsilon_f\; B_f \qquad\qquad\qquad\text{eq. 14}$$

559 The biomass for shrubs at the beginning of the current growing season was a fix fraction

560 (0.05) of past year biomass produced, while for grasses, biomass was the balance

561 between biomass produced in the growing season minus biomass lost in autumn and

562 winter.

563 2. *Simulations*

564   *2.1. Biodiversity gradient*

565   We estimated the biodiversity effect as the difference between observed and

566 expected ANPP (eq 15) (Loreau and Hector 2001). The expected value (second term in

567 eq. 15) was the product of the proportion of life form *f* in the mixture (term in brackets)

568 and its ANPP as monoculture. For example, if the proportion of grasses was 50% at the

569 end of autumn, the expected value in the mixture was half of grasses ANPP growing as a

570 monoculture.

571     $\text{Biodiversity effect} = \sum ANPP_{f.Mix} - \sum \left(\dfrac{B_{f.Mix}}{B_{SH.Mix} + B_{GR.Mix}} \right) ANPP_{f.Mono}$ eq. 15

572 *Mix* and *Mono* suffixes indicate values obtained from mixtures and monocultures

573 respectively. Finally, we estimated sampling effect (eq. 16) (Loreau and Hector 2001).

574     $\text{Sampling effect} = 2 * \text{cov} \left(\dfrac{ANPP_{f.Mix}}{ANPP_{f.Mono}} - \dfrac{B_{f.Mix}}{B_{SH.Mix} + B_{GR.Mix}}, ANPP_{f.Mono} \right)$ eq. 16

575   *2.2. Resource partitioning gradient*

576 We defined resource partitioning as the mean fraction of root non-overlap between life

577 forms (eq. 17)

578     $\text{root overlap} = 1 - [\sum (root_{SH-y} - root_{GR-y})^2 / 2]^{1/2}$ eq. 17

579

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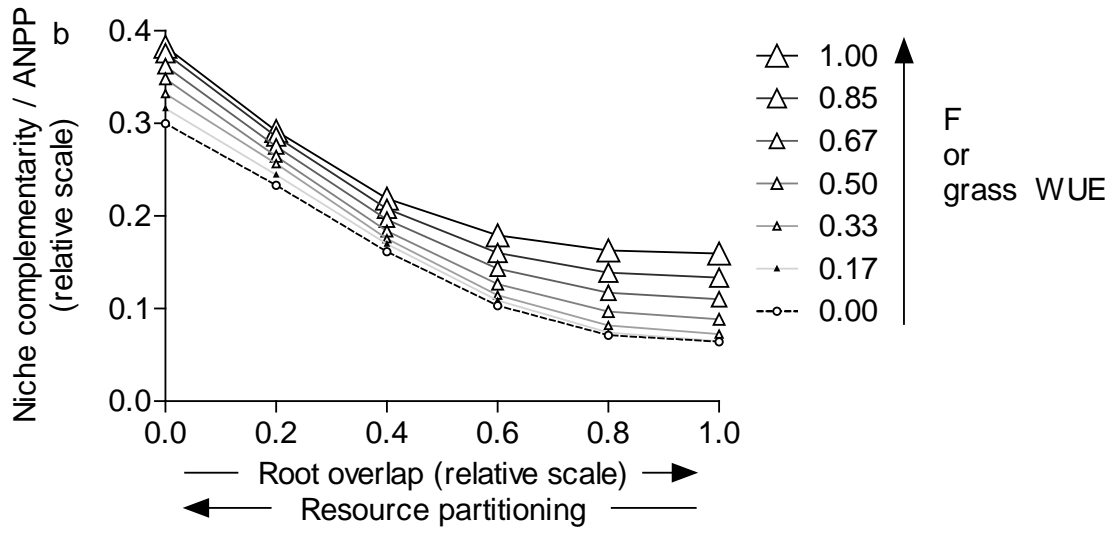
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601 **Supplemental Information Figures**

602

603 **Figure S1: Influence of increased WUE for grasses and root overlap on niche**

604 **complementarity.** Niche complementarity was estimated using Loreau and Hector

605 (2001) method. Root overlap (RO) and increased grass WUE simulated resource

606 partitioning (RP) and facilitation (F) gradients. Lines depict simulations with the same

607   root overlap and same increased WUE for grasses. Niche complementarity was expressed

608   as a fraction of ANPP.

609

610