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**Pedro Flombaum, Osvaldo E. Sala &
Edward B. Rastetter**

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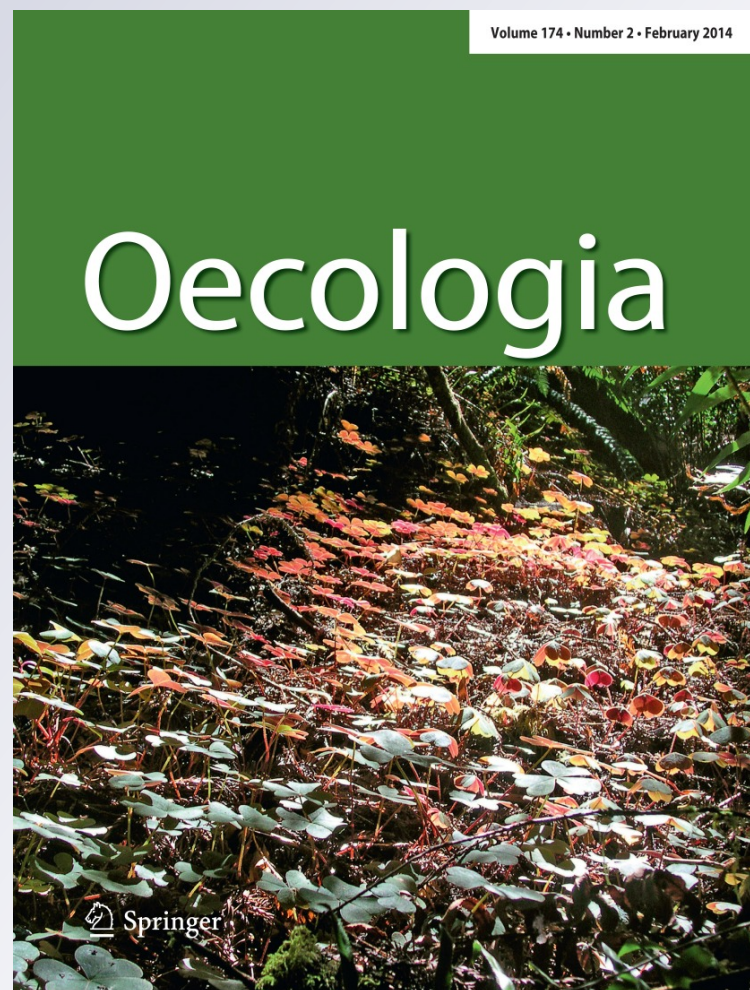
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Interactions among resource partitioning, sampling effect, and facilitation on the biodiversity effect: a modeling approach

Pedro Flombaum · Osvaldo E. Sala ·
Edward B. Rastetter

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Abstract Resource partitioning, facilitation, and sampling effect are the three mechanisms behind the biodiversity effect, which is depicted usually as the effect of plant-species richness on aboveground net primary production. These mechanisms operate simultaneously but their relative importance and interactions are difficult to unravel experimentally. Thus, niche differentiation and facilitation have been lumped together and separated from the sampling effect. Here, we propose three hypotheses about interactions among the three mechanisms and test them using a simulation model. The model simulated water movement

through soil and vegetation, and net primary production mimicking the Patagonian steppe. Using the model, we created grass and shrub monocultures and mixtures, controlled root overlap and grass water-use efficiency (WUE) to simulate gradients of biodiversity, resource partitioning and facilitation. The presence of shrubs facilitated grass growth by increasing its WUE and in turn increased the sampling effect, whereas root overlap (resource partitioning) had, on average, no effect on sampling effect. Interestingly, resource partitioning and facilitation interacted so the effect of facilitation on sampling effect decreased as resource partitioning increased. Sampling effect was enhanced by the difference between the two functional groups in their efficiency in using resources. Morphological and physiological differences make one group outperform the other; once these differences were established further differences did not enhance the sampling effect. In addition, grass WUE and root overlap positively influence the biodiversity effect but showed no interactions.

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P. Flombaum
Departamento de Ciencias de la Atmósfera y los Océanos,
Centro de Investigaciones del Mar y la Atmósfera, Instituto
Franco-Argentino sobre Estudios de Clima y sus Impactos,
Consejo Nacional de Investigaciones Científicas y Tecnológicas,
Universidad de Buenos Aires, Unidad Mixta Internacional
(CONICET/UBA-FCEN/UMI-CNRS), Buenos Aires, Argentina

P. Flombaum (✉)
Departamento de Ciencias de la Atmósfera y los Océanos
(DCAO), Universidad de Buenos Aires, Pabellón II Piso 2,
Ciudad Universitaria, C1428EGA Buenos Aires, Argentina
e-mail: pflombaum@cima.fcen.uba.ar

O. E. Sala
School of Life Sciences and School of Sustainability, Arizona
State University, Phoenix, AZ, USA

E. B. Rastetter
The Ecosystem Center, Marine Biological Laboratory, Woods
Hole, MA, USA

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Introduction

Understanding the relationship between biodiversity and ecosystem functioning is crucial to assess some of the consequences of species loss (Chapin et al. 2000). In this field, a central hypothesis is that the rate of ecosystem processes increases with biodiversity (Vitousek and Hooper 1993; Schlapfer and Schmid 1999). To test this hypothesis, manipulative experiments created monocultures and species mixtures representing the low and high end of biodiversity

gradients, and estimated aboveground net primary production (ANPP), an integrative variable representing ecosystem processes. These studies found, in general, a positive relationship between plant-species richness and ANPP (Tilman et al. 1996; Hector et al. 1999; Flombaum and Sala 2008), which is accounted for by three different mechanisms: resource partitioning, facilitation among species (together known as niche complementarity), and sampling effect (Huston 1997; Tilman 1997; Loreau 2000; Loreau and Hector 2001; Mulder et al. 2001; Flombaum and Sala 2012). Resource partitioning is the use of different resources by different species as a result of evolutionary niche separation. In high-diversity ecosystems, fine resource partitioning results in high ANPP because more species means that more traits are expressed that can therefore exploit resources more thoroughly (Tilman et al. 1997). Facilitation, here used as synonymous with positive interactions, represents benefits provided by one species that can increase the effective niche of other species by habitat amelioration, enhanced recruitment or predation refuge; and consequently results in higher ANPP (Bruno et al. 2003). The sampling effect in biodiversity and ecosystem-functioning experiments is associated with the chance of including the most productive species in a randomly assembled mixture (Huston 1997; Tilman 1997). The sampling effect is based on the idea that in a community there are always a few species that outperform the others. Therefore, ANPP increases with species richness just because of the higher probability of including outperforming species in the mixture.

The individual effects of resource partitioning, facilitation and sampling effect are well established; on the contrary, the interactions among the three of them are uncertain. Especially, the effects of resource partitioning and facilitation on the sampling effect are poorly understood.

Hypothesis 1 Resource partitioning positively affects sampling effect because, under conditions of low resource partitioning, it would be difficult for a single species to outperform all others. For the sampling effect to occur, a species needs to outperform all others in the mix; and the probability of the existence of such species increases as differences among species increase.

Hypothesis 2 Facilitation positively affects the magnitude of the sampling effect because the benefits from facilitation could be the characteristic that determines one species outperforming others. Therefore, facilitation increases the probability that a recipient of facilitation benefits sufficiently to outperform all other species in the mix.

Hypothesis 3 The interaction between resource partitioning and facilitation has no influence on the sampling and

biodiversity effects. Resource partitioning and facilitation result from independent morphological and physiological characteristics of individual species, hence their effect on the biodiversity effect is independent.

Interactions among resource partitioning, sampling effect and facilitation would be difficult to reveal using field experimentation because the number of experimental units would be prohibitive and because of the difficulty disentangling effects of facilitation and resource partitioning. Consequently, facilitation is commonly lumped with resource partitioning and is differentiated from the sampling effect (Loreau and Hector 2001; Mulder et al. 2001; Vanellander et al. 2009; Crawford and Whitney 2010). Here, we developed a simulation model of water movement and ANPP in an arid ecosystem to test hypotheses 1–3. We modified plant-life-form richness, root distribution, and water-use efficiency (WUE) to generate three independent gradients of biodiversity, resource partitioning, and facilitation. Specifically, we altered root overlap between shrubs and grasses to represent different degrees of resource partitioning. Increasing root overlap represents decreasing resource partitioning since both plant functional types explore the same soil resources. We modified WUE of grasses in the presence of shrubs as a way of representing the physiological outcome of the facilitation resulting from the protective effect of shrubs over grasses. Increased grass WUE in the presence of shrubs represents high facilitation. Using the simulation model, we estimated: (1) the biodiversity effect as the difference in modeled and expected ANPP, and (2) the sampling effect using Loreau and Hector's method (2001).

We focused on arid ecosystems because they are largely influenced by facilitation and resource partitioning (Sala et al. 1989; Bertness and Callaway 1994; Bruno et al. 2003; Craine et al. 2003; Flombaum and Sala 2012) and because their low diversity provides ideal models to study biodiversity and ecosystem functioning relationships (Flombaum and Sala 2008). We parameterized our model to represent major ecological variables in an arid ecosystem, the Patagonian steppe. We chose this particular site because we had data from a manipulative experiment that assessed the effect of biodiversity on ecosystem functioning (Flombaum and Sala 2008, 2012) and reliable information on climate, ecosystem structure and functioning (Aguiar and Sala 1994; Jobbágy and Sala 2000). For the sake of simplicity, we only considered the main life-forms of the Patagonian steppe, grasses and shrubs, that account for 95 % of ANPP (Jobbágy and Sala 2000), use different sources of water (Sala et al. 1989), and establish facilitative interactions (Aguiar and Sala 1994).

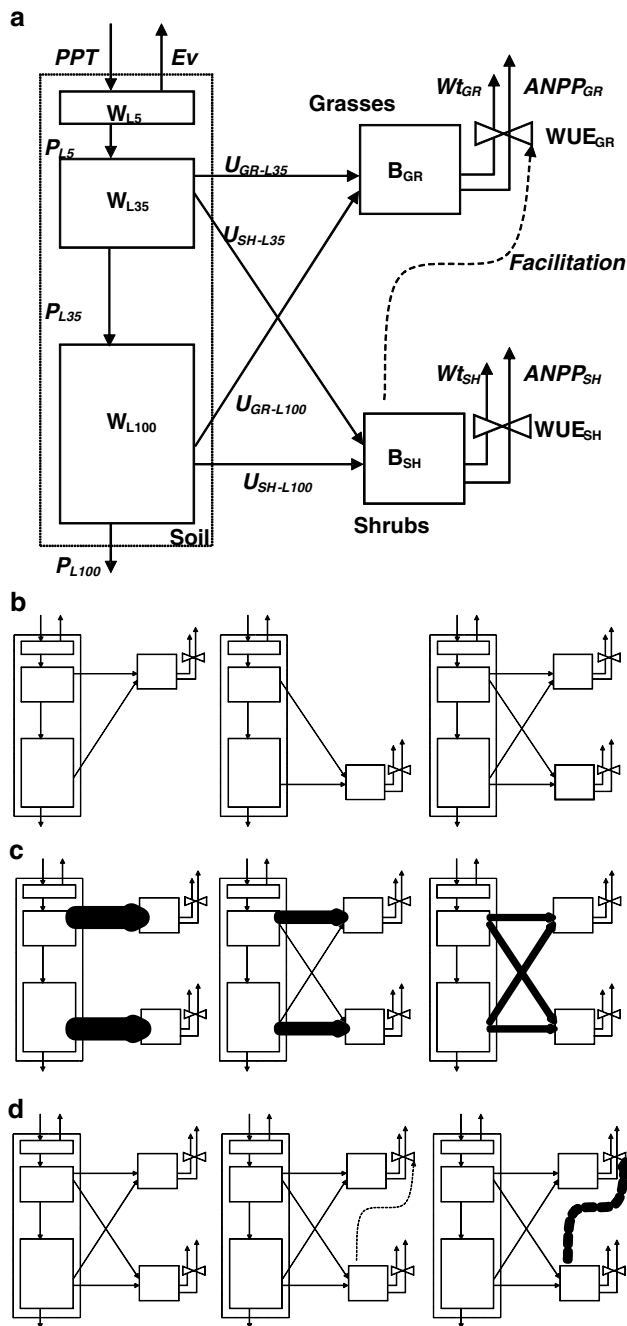


Fig. 1 Model description and experiments of **b** life-form richness, **c** root overlap, and **d** increased grass water-use efficiency (WUE). **a** Model components, fluxes and controls. *Solid arrows and italics* Flows, *dashed arrows* controls, *solid boxes* state variables, *dotted box* group soil components. *PPT* precipitation, *Ev* evaporation, *ANPP* aboveground net primary production, *L5* topsoil layer, *L35* mid soil layer, *L100* bottom soil layer, *SH* shrubs, *GR* grasses, *P* water percolation, *W* water content, *U* water uptake, *W* plant-water status, *WUE* water-use efficiency, *B* plant biomass. **b** Simulated biodiversity gradient with grass monoculture (*left*), shrub monoculture (*middle*), and mixture (*right*). **c** Simulated low, mid, and high root overlap representing a high, mid and low resource partitioning gradient (from *left* to *right*). The *thickness* of the *arrow* indicates the proportion of root in each layer. **d** Simulated increase in grass WUE representing a facilitation gradient. From *left* to *right*: null, mid and high grass WUE; the *thickness* of the *arrow* indicates the amount of facilitated WUE perceived by grasses in the presence of shrubs

percolation (Fig. 1a). Evaporation only occurred from the top layer where no root was present. Plants uptake water from the lower two soil layers and their WUE linked transpiration to biomass production (Fig. 1a). A full description of the model equations is available in Supplemental Information 1.

Simulations

We simulated gradients of biodiversity, root-overlap between grasses and shrubs and grass WUE in the presence of shrubs (Fig. 1b–d). The model observed output was biomass production by grasses and shrubs. We estimated the biodiversity effect as the difference between the ANPP of the grass-shrub mix and the ANPP predicted based on the productivity of the grass or shrub monocultures. Then, we split the biodiversity effect into the sampling effect using Loreau and Hector’s additive partitioning scheme (2001).

Parameter adjustment

We tuned parameters (senescent biomass constant, WUE, ratio between aboveground and belowground biomass, water absorption rate, saturation, wilting point, temperature constant, water conductance constant for evaporation and percolation; Table 1) to reproduce ANPP and ecosystem WUE for the Patagonian steppe. We set saturation and wilting point parameters with standard values for sandy soils; and the ratio between aboveground and belowground biomass, and the depth of the three soil layers (*L5*, *L35*, and *L100*) with typical values for the Patagonian steppe (Table 1). The other parameter values were set arbitrarily and adjusted in successive iterations to improve the fit. For the calibration, shrub roots were restricted to the bottom layer, and grass roots to the middle layer (Table 1), representing a case of zero root overlap.

Our model reproduced long-term averages for the Patagonian steppe. We simulated grass and shrub ANPP

Materials and methods

Model description

We developed a model that simulates soil water movement and ANPP dynamics in the Patagonian steppe with daily time step forced with precipitation and temperature records. The model source code was written in Object Pascal using IDE Lazarus version 1.0 (www.lazarus.freepascal.org). In the model, water entered the system as rainfall, moved downward through three soil layers, and exited the system as soil evaporation, plant transpiration, and deep

Table 1 Model parameters and their influence on mean aboveground net primary production (ANPP)

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-L35} ^b	1	0				
root _{F-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)	
T_s (°C)						4 (-0.4)
α_{ev} (day ⁻¹)						0.1 (-1.1)
α_{per} (day ⁻¹)						1 (0.2)

Values for each parameter were set to represent mean ANPP and rain use efficiency for the Patagonian steppe. In *parentheses*, percent change in mean ANPP with a 10 % increase in the parameter indicating the sensitivity of the model

ε Senescent biomass constant, WUE water-use efficiency, γ ratio between above and belowground biomass, δ water absorption rate, $root$ proportion of root in a layer, tB aboveground green biomass, $sat.$ water retention constant for saturation, $wil.$ water retention constant for wilting point, h height of the soil layer, T_s temperature constant, α_{ev} water conductance constant for evaporation, α_{per} water conductance constant for percolation, $L5$ topsoil layer, $L35$ mid soil layer, $L100$ bottom soil layer

^{a, b, c} Values that changed in the experiments where we modified grass WUE to represent changes in facilitation and where we changed root overlap to represent changes in resource partitioning

using 19 years of climatic data, and compared them with 15 and 19 years of grass and shrub field observations of ANPP (Jobbágy and Sala 2000; Flombaum and Sala 2009). Our model simulated a 3.5 and 2.5 % higher than observed mean total ANPP and mean rain-use efficiency, respectively (Table 2); ANPP for grasses and shrubs was 1.1 and 2.0 g m⁻² year⁻¹ higher; however, none of these mean values were statistically different ($p > 0.05$; Table 2). Also, the model reproduced the observed relationship between mean annual precipitation and ANPP for grasses, shrubs, and both combined (Fig. 2). Finally, we performed a sensitivity analysis in which we modified each of the parameters by $\pm 10\%$ and estimated the percent of change in mean ANPP using 19 years of climatic data. No parameter significantly changed the mean ANPP (t -test; $p > 0.05$). The parameters of WUE for shrubs (WUE_{SH}) and grasses (WUE_{GR}), and the saturation point of the middle layer (sat_{L100}) had the largest impact on ANPP. ANPP increased by 5.5, 5.2 and 5.5 % with a 10 % increase in WUE_{SH} , WUE_{GR} and sat_{L100} , respectively (Table 1: values in parentheses).

The focus of this exercise was not to reproduce the Patagonian steppe functioning from first principles but rather to mimic its dynamics to evaluate the effects of root overlap and grass WUE on the biodiversity and sampling effect. Based on the modeled and observed mean values for the Patagonian steppe (Table 2), the relationship between the sensitivity of the parameters (Table 1) and the relationship between ANPP and precipitation (Fig. 2), we found

Table 2 Modeled and observed mean ANPP and rain use efficiency for the Patagonian steppe

	Modeled	Observed
ANPP total (g m ⁻² year ⁻¹)	59.3 \pm 20.8	56.3 \pm 14.8
ANPP grasses (g m ⁻² year ⁻¹)	28.0 \pm 9.4	26.9 \pm 9.7
ANPP shrubs (g m ⁻² year ⁻¹)	31.3 \pm 13.3	29.3 \pm 9.0
RUE (g m ⁻² mm H ₂ O ⁻¹)	0.40 \pm 0.14	0.39 \pm 0.11

We modeled ANPP using 19 years of climatic data (i.e., temperature and precipitation) for Rio Mayo field station, Chubut, Argentina. Observed field estimations of ANPP were obtained from the same locality, and mean values are based on 15 and 19 years of samples for shrubs and grasses, respectively (Jobbágy and Sala 2000; Flombaum and Sala 2009). Simulated mean \pm 1 SD values were obtained based on 19 years of climatic data; observed mean \pm 1 SD values represent the mean of 15 and 19 years for shrubs and grasses, respectively

ANPP Aboveground net primary production

RUE Rain-use efficiency

Values did not differ statistically ($p > 0.05$)

that our model was well suited to reproduce major patterns of the Patagonian steppe.

Biodiversity gradient

We simulated a gradient of life-form richness with grass and shrubs growing as monocultures or together as a mixture (Fig. 1b). Monocultures and mixtures started with the same initial biomass, reproducing the design of a

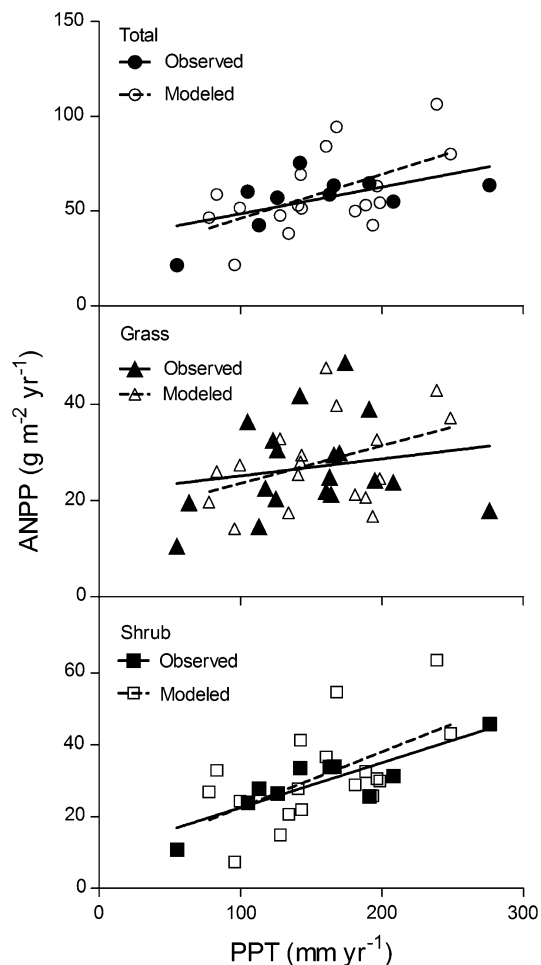


Fig. 2 Relationship between aboveground net primary production (ANPP) and mean annual precipitation (PPT) for life-forms combined, grasses, and shrubs. Simulated ANPP was obtained using our model and 19 years of climatic data. Observed ANPP was obtained from Jobbágy and Sala (2000) and Flombaum and Sala (2009). Climatic and ANPP field observations were obtained from the same locality in Rio Mayo field station, Chubut, Argentina

replacement-series experiment. We estimated ANPP for 3 consecutive years (1986–1988), with each growing season starting at the end of autumn. We initialized the mixture at 50 % grasses and 50 % shrubs in the first year, and set the proportions at the beginning of subsequent years according to the productivity of the life-form in the preceding year. Life-form proportions were used to estimate the biodiversity and the sampling effects (Supplemental Information 2.1).

Resource partitioning gradient

We simulated a gradient of root overlap to represent resource partitioning. We modified grass and shrub root distributions in the middle and bottom soil layers (Fig. 1c)

(Supplemental Information 2.2). The root overlap gradient had a value of zero when grasses had their roots in the middle layer and shrubs in the bottom layer ($root_{GR-L35} = 1$, $root_{GR-L100} = 0$, $root_{SH-L35} = 0$, $root_{SH-L100} = 1$), and a value of one when grasses and shrubs had exactly the same root distribution with half of their roots in each layer ($root_{SH-L100} = root_{GR-L100} = root_{SH-L35} = root_{GR-L35} = 0.5$).

Facilitation gradient

Facilitation was defined as the amelioration on physical conditions for grasses by the presence of shrubs. We represented facilitation as an increase in grass WUE when grasses occur in the mix with shrubs (Fig. 1d), reproducing an effect observed in arid ecosystems (Bertness and Callaway 1994; Armas and Pugnaire 2005). We changed the grass WUE parameter to create the gradient. WUE for grasses growing in monoculture was $0.65 \text{ g m}^{-2} \text{ mm H}_2\text{O}^{-1}$, and grass WUE increased in steps of 0.05 up to $0.95 \text{ g m}^{-2} \text{ mm H}_2\text{O}^{-1}$ in the mix. The minimum value of facilitation, $0.65 \text{ g m}^{-2} \text{ mm H}_2\text{O}^{-1}$, resulted from parameter tuning to reproduce mean values in the Patagonian steppe (Table 1). We arbitrarily set the maximum WUE at $0.95 \text{ g m}^{-2} \text{ mm H}_2\text{O}^{-1}$. Finally, we rescaled the gradient from zero to one, to compare with the resource partitioning gradient.

Data analysis

We performed a multiple regression analysis with biodiversity effect or sampling effect as response variables, and root overlap, increased grass WUE, and their interaction as predictors using MATLAB (Mathworks, MA). The use of a zero to one scale for root overlap and grass WUE allowed us to compare the relative effects of each predictive variable. We reported regression parameters as significant if their 95 % confidence interval did not include zero.

Results

The sampling effect, expressed as a fraction of ANPP, was on average unrelated to root overlap, which simulated resource partitioning. The sampling effect increased with increased grass WUE, which simulated facilitation (Fig. 3a; Table 3). Most interesting is that there was a significant interaction between root overlap and WUE so as facilitation increased the effect of resource partitioning on sampling effect decreased. When there was no facilitation of shrubs on grasses, resource partitioning increased sampling effect. On the contrary, when facilitation was maximal, resource partitioning decreased the sampling effect.

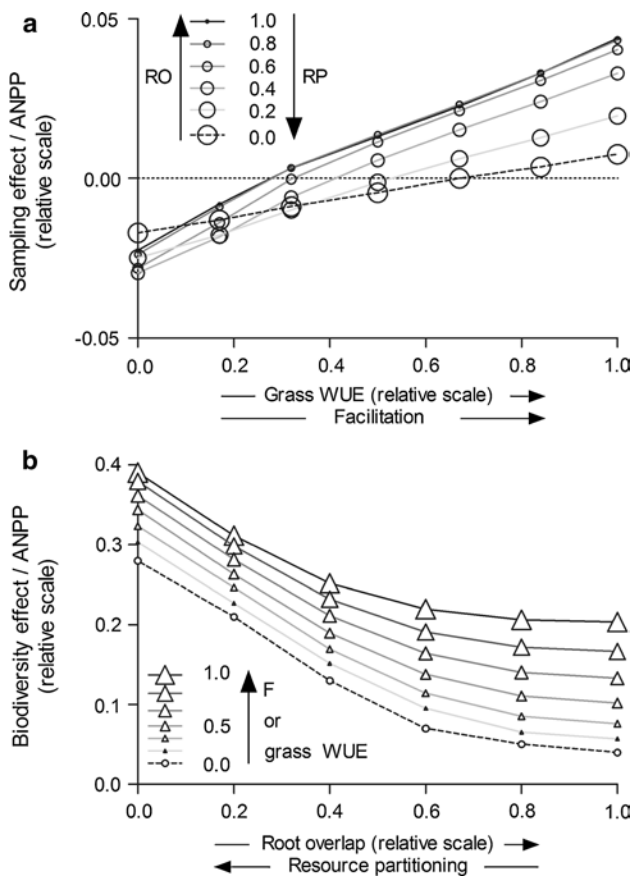


Fig. 3 Influence of **a** increased water use efficiency (WUE) for grasses and **b** root overlap (RO) on the sampling and the biodiversity effect. RO and increased grass WUE simulated resource partitioning (RP) and facilitation (F) gradients. Lines in **a** and **b** depict simulations with the same RO and same increased WUE for grasses. The sampling and the biodiversity effect were expressed as a fraction of aboveground net primary production (ANPP)

Table 3 Root overlap (RO) and grass WUE influence on the sampling effect (SE) and the biodiversity effect (BE)

	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 \times grass WUE	0.032 ± 0.012	0.064 ± 0.072
MS	0.005	0.120
F	251.9	167.9

Values represent the slopes $\pm 95\%$ confidence interval of a multiple linear regression. Values in *italics* did not include the zero within the 95% confidence interval

The biodiversity effect, which was expressed relative to ANPP, increased with root overlap and grass WUE, which simulated gradients of resource partitioning and facilitation, respectively (Fig. 3b). The biodiversity effect

reached its highest value when root overlap was minimal and grass WUE was maximal. Changes in root overlap had larger effects than grass WUE. The biodiversity effect increased seven times between 1 and 0 root overlap (i.e., low and high resource partitioning) at 0 increase in grass WUE (Fig. 3b: dashed line). Also, the biodiversity effect increased five times between the 0 and 1 grass WUE at 1 root overlap (i.e., no resource partitioning) (Fig. 3b: circle vs. largest triangle). In addition, the multiple regression slope of root overlap was 2.7 times higher than that of grass WUE (Table 3). Finally, we observed no interaction between root overlap and grass WUE on the biodiversity effect (Table 3).

Discussion

Our results indicated that, on average, root overlap (simulating resource partitioning) did not affect sampling effect but grass WUE (simulating facilitation) did. Most interesting is the interactive effect of resource partitioning and facilitation on the sampling effect. As facilitation increased, the effect of resource partitioning on sampling effect decreased. These results suggest that the magnitude of the sampling effect depends on the functional differences among functional groups (or species) that make one group outperform the other. Differences between shrubs and grasses in our experiment result from either facilitation or resource partitioning, which compensate for each other. When both groups have the same root patterns the effects of differential WUE are responsible for the sampling effect. On the contrary, when there is no facilitation root depth is the variable that determines that one species outperforms the other and determines the magnitude of the sampling effect.

Both facilitation and resource partitioning positively affected the biodiversity effect (Fig. 3b) but there was no interaction among them supporting hypothesis 3. Root overlap and grass WUE affect the ability of the community to utilize resources and therefore affect the biodiversity

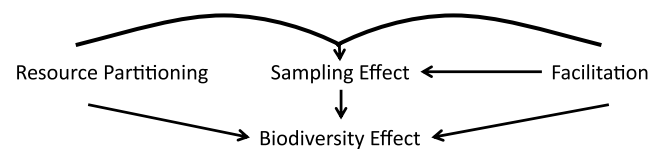


Fig. 4 Direct and indirect influences on the biodiversity effect. The influences identified in this figure result from an experiment using a simulation model that mimics the Patagonian steppe. The experiment was a full factorial design with root overlap and grass water use efficiency representing resource partitioning and facilitation. Facilitation and its interaction with resource partitioning indirectly influenced the biodiversity effect through the sampling effect

effect but they are not related to each other. Decreased root overlap increases water capture and increases WUE efficiency by reducing transpiration per unit of production.

Resource partitioning and facilitation (Loreau and Hector 2001) directly influenced the biodiversity effect, in agreement with empirical results (Mulder et al. 2001; Flombaum and Sala 2012). In addition, facilitation and its interaction with resource partitioning indirectly influenced the biodiversity effect through the sampling effect (Fig. 4). In our simulation experiment, the sampling effect was a minor fraction of the biodiversity effect (Fig. 3) similar to what was observed for the Patagonian steppe (Flombaum and Sala 2008).

Our modeling experiments provided a possible explanation for results of biodiversity and ecosystem functioning experiments performed with seeded ecosystems. Experiments showed that the biodiversity effect increased with time mostly because of an increase in niche complementarity, and at the same time they showed an accompanying reduction in the sampling effect (van Ruijven and Berendse 2005; Fargione et al. 2007). Resource partitioning gradients, like the one described here, could occur through time from early to late successional stages in sowed experiments as phenotypic characteristics get fully expressed through time (Sala 2001), so our decreasing root overlap could be replaced by time in seeded experiments. Our simulations suggested that facilitation and resource partitioning were the major mechanisms of the biodiversity effect, although in early successional stages (i.e., low resource partitioning) their effect occurred indirectly through the sampling effect (Figs. 3, 4).

The simulated facilitation-partitioning interaction resulted from the asymmetry of the relationship between grasses and shrubs. Grasses were benefited by shrubs by reduced evaporative demand resulting in higher WUE. Simultaneously, the increased grass growth and transpiration reduced the amount of water that reaches the lower soil layers. Consequently, under conditions of high resource partitioning and when shrubs absorb water only from lower layers, the facilitation effect on grasses produced a negative effect on shrub water availability and growth. There is empirical evidence of a facilitation shifting to inhibition depending on the life stage, physiology and environment (Callaway and Walker 1997; Graff et al. 2007). The pattern simulated here, in which the species that receives the benefit negatively impacts the species that provides the benefit, has also been observed in grass and legume ecosystems (Temperton et al. 2007; Marty et al. 2009).

Disentangling the relative importance and interactions of the three mechanisms of the effect of biodiversity on ecosystem functioning is important from the basic understanding of the relationships between community structure and ecosystem functioning and from the conservation point

of view. Our manipulation of grass WUE and root overlap representing gradients of facilitation and resource partitioning in a modeling experiment adds a complementary perspective to previous work that manipulated resource partitioning, competitive interactions or both (Yachi and Loreau 2007; Carroll et al. 2011; Verón et al. 2011; Loreau et al. 2012). Field experiments that specifically addressed facilitation and resource partitioning on biodiversity and ecosystem functioning found little or no influence of facilitation (Gross et al. 2007; Northfield et al. 2010), which highly contrasts with our modeling perspective. As a whole, our modeling results show a much larger effect of facilitation and resource partitioning than the sampling effect, highlighting the need for conserving biodiversity for the maintenance of ecosystem services.

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