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# Effects of plant species traits on ecosystem processes: experiments in the Patagonian steppe

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*Abstract*. Several experiments have shown that aboveground net primary productivity increases with plant species richness. The main mechanism proposed to explain this relationship is niche complementarity, which is determined by differences in plant traits that affect resource use. We combined field and laboratory experiments using the most abundant species of the Patagonian steppe to identify which are the traits that determine niche complementarity in this ecosystem. We estimated traits that affect carbon, water, microclimate, and nitrogen dynamics. The most important traits distinguishing among species, from the standpoint of their effects on ecosystem functioning, were potential soil nitrification, rooting depth, and soil thermal amplitude. Additionally, we explored the relationship between trait diversity and aboveground net primary production (ANPP) using a manipulative field experiment. ANPP and the fraction of ANPP accounted for by trait diversity increased with number of traits. The effect of trait diversity decreased as the number of traits increased. Here, the use of traits gave us a mechanistic understanding of niche complementarity in the Patagonian steppe.

*Key words: aboveground net primary production (ANPP); niche complementarity; rooting depth; soil nitrification; soil thermal amplitude; trait diversity.*

## INTRODUCTION

Ecologists' interest in understanding the role of biodiversity on ecosystem functioning has increased since they realized that global biodiversity was being drastically altered by anthropogenic activities and that it was urgent to address its consequences. The central hypothesis of the effect of biodiversity on ecosystem functioning states that decreases in species richness would result in decreases in rates of ecosystem processes (Vitousek and Hooper 1993). The first controlled tests of this hypothesis were based on experimental plant species richness gradients, which were created in artificial ecosystems by sowing different numbers and combinations of species (Tilman et al. 1997*a*, Hector et al. 1999). These experiments yielded consistent patterns that as number of species increased the rate of net primary production increased up to a point when ecosystem response saturated and that niche complementarity accounted for most observed effects of species richness on ecosystem functioning (Loreau and Hector 2001). Moreover, an experiment in a natural ecosystem in Patagonia showed a biodiversity effect that was significantly stronger than previously reported from experiments with synthetic communities and identified niche complementarity as the dominant mechanism accounting for the increase in production with species richness (Flombaum and Sala 2008). The effect of niche complementarity on ecosystem functioning results from larger amounts of resources used in ecosystems containing species with different ecological niches (Tilman et al. 1997*b*). The ecological niche of a species depends on the collection of its traits, and these are shaped by evolutionary processes that maximize species fitness (Chase and Leibold 2003). Examples of species differentiation in traits occur as a result of long-term species interactions with each other (Brown and Wilson 1956), or as a result of local adaptation that occur in coexisting populations of different species exposed to local environmental conditions (Kawecki and Ebert 2004). Niche complementarity has been related to resource use but could also occur via other dimensions of the ecological niche; here we will refer to resource-use niche complementarity. Other factors that may account for the observed effects of species richness on ecosystem functioning are positive interactions and sampling effect (Huston 1997, Tilman et al. 1997*b*).

Although niche complementary is one of the major mechanisms accounting for the effect of biodiversity on ecosystem functioning, it is still unclear how niche complementarity occurs, what characteristics of species result in niche complementarity, and ultimately, what species traits affect the functioning of ecosystems. The

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link between niche complementarity and ecosystem functioning has been established through analytical tools (Loreau and Hector 2001, Fargione et al. 2007, Flombaum and Sala 2008) and, just recently, using direct estimates of niche complementarity (Cardinale 2011). Here, we specifically addressed the following questions. (1) How does niche complementarity in the Patagonian steppe occur? (2) What are the species traits that account for most of the observed niche complementarity? And finally, since species affect ecosystem processes through their traits, (3) how does trait diversity affect ecosystem functioning?

Here, we report on a study of plant species traits and their effect on ecosystem functioning. We used the Patagonian steppe as a model ecosystem, because its low natural diversity makes it relatively simple to study, and because the relationship between plant species richness and biodiversity has been shown to be driven by species niche complementarity (Flombaum and Sala 2008).

## MATERIALS AND METHODS

### *Study site*

Our study site is located in the Patagonian steppe, Southern South America (see Plate 1). We worked in INTA Río Mayo, Argentina (45°41′ S 70°16′ W), where the climate is semiarid with 170 mm of annual precipitation, which occurs mostly during fall and winter. Average monthly temperatures range from 2°C to 14°C for winter and summer, respectively. Soils are coarse textured with gravel and stones. Vegetation corresponds to the Occidental floristic district characterized by two life forms, grasses and shrubs, and relatively low species richness. Three grass species (*Stipa speciosa* Trin et Ruprecht, *Stipa humilis* Cav., and *Poa ligularis* Nees ap. Steud) and three shrub species (*Mulinum spinosum* (Cav.) Pers., *Adesmia volckmanni* (Philippi), and *Senecio filaginoides* DC) account for 97% of aboveground net primary productivity (Flombaum and Sala 2008).

### *Plant species traits that affect ecosystem functioning*

For all the dominant plant species of the Patagonian steppe, we evaluated relative growth rate, potential soil respiration, rooting depth, plant phenology, soil thermal amplitude, potential soil net nitrification and net ammonification, and nitrogen-form relative preference, which are plant traits that influence carbon, water, microclimate, and nitrogen dynamics in an ecosystem (see Appendix A for a detailed description of methods). We assessed species relative growth rate to investigate how species could influence net primary production, and potential soil respiration as a pathway by which species can influence soil carbon release to the atmosphere. Carbon fixation and release are processes related to the energy flow and, in arid ecosystems, these processes are closely related to water availability (Yahdjian et al. 2006). We considered plant species influence on water flow from the soil to the atmosphere by addressing rooting depth, which gives an indication of a plant capacity to draw down soil moisture with depth (Eviner and Chapin 2003), and plant annual phenological cycles, which have important effects on soil seasonal water demand and carbon sequestration (Eviner and Chapin 2003). Plant species effects on soil microclimate can have a large effect on belowground biological activity. We evaluated the thermal amplitude below different species, which can alter the biological activity rate (Smith et al. 2003). We also evaluated plant species effects on nitrogen mineralization, the main pathway by which organic nitrogen becomes available to plants and soil microorganisms, and ammonium and nitrate relative absorption by plants because of their differential distribution in the soil profile. The importance of traits in affecting the relationship between trait diversity and ecosystem functioning depends on the distribution of traits among species. If all species in a community have a similar level for a trait, that trait will explain little of the effect of biodiversity. On the contrary, traits that have different levels for different species should have a large contribution to the effect of biodiversity on ecosystem functioning. To compare trait distribution among species, we made traits relative to minimum and maximum levels and therefore they ranged between 0 and 1. We divided this scale into six levels, and used $H'$ (modified Shannon index) to examine the frequency of species occurring in each level.

### *Trait-diversity gradients*

We used a plant species diversity gradient experimentally created in Patagonia (Flombaum and Sala 2008) to define various trait diversity gradients. The gradient of plant richness had 1, 2, 4, and 6 species with all 6, 15, 15, and 1 possible assemblages (37 in total) using the same six species mentioned in *Materials and methods: Study site*. We generated a species richness gradient by removing plant species, and we equalized total plant cover on the plots by removing variable portions of individuals that were not targeted for removal (Flombaum and Sala 2008). In this way, our removal disturbance was the same among all plots. This approach resulted in experimental plots having the same vegetation cover along the gradient, but differing in species number and assemblages (Flombaum and Sala 2008).

We redefined the plant species richness gradient into various trait-richness gradients. Here, it is important to distinguish between traits, which are characters, and levels, which refer to specific values of traits. For example, rooting depth is a trait, and 40 cm deep is the level of *S. speciosa* for rooting depth. Species were considered to have different levels if their means were different. For example, the trait plant phenology had species in three levels corresponding to the means 5, 7, and 12 months. We used single traits and also combinations of traits to define various trait gradients. We evaluated 255 trait richness gradients that resulted from combining one to eight traits. For example, we evaluated a richness gradient of plant phenology, another richness gradient of plant phenology combined with potential soil respiration, another for all traits combined, and so on.

With the list of species assemblages (from the species diversity gradient), and each species assigned to a level (based on its mean), we redefined the species richness gradient into trait richness gradients. For each species assemblage, we counted the number of levels for a trait. For example, the two-species assemblage of *S. speciosa* and *P. ligularis* counted as one level of plant phenology (since both species had 12 months of green leaves); while the two-species assemblage of *S. speciosa* and *M. spinosum* counted as two levels of plant phenology (since species had 12 and 7 months of green leaves; Appendix B). In trait richness gradients that combined more than two traits, we counted the total number of levels per assemblage; for example, in the gradient that combined plant phenology and rooting depth, the two-species assemblage of *S. speciosa* and *P. ligularis* counted as three levels (Appendix B). In all trait richness gradients, one-species plots (monocultures) had the lowest level of trait richness, and the mixture with species richness of six (the highest species richness) had the highest combination of trait levels; combinations with two and four species could be closer to monocultures or to the six species mixture.

In each experimental plot, we estimated aboveground net primary production (ANPP) with four, 5 m long, equally spaced, parallel lines. We recorded vegetation cover on the lines and used a nondestructive method that correlated cover and biomass to estimate ANPP (Flombaum and Sala 2007). ANPP was estimated as the increase in biomass from early spring (September 2002) to summer.

### *Statistical analyses*

To compare differences in species traits, we conducted one-way analyses of variance (ANOVA) and a posteriori Fisher's LSD contrast, with the exception of phenology and rooting depth, for which we considered that two species differed in rooting depth if the difference was more than 30 cm and that species differed in plant phenology if the difference in the extent of the period with green leaves was more than three months. Also, we performed a priori contrasts to compare between grasses and shrubs. Using the species average for each trait, we performed trait correlations and a principal components analysis (PCA). Last, to assess the effect of trait diversity on ANPP we estimated the portion of variance explained ($R^2$) by trait diversity, and estimated the best fit between $R^2$ and the number of traits considered in the trait-diversity gradients.

## Results

### *Plant species traits that affect ecosystem functioning*

We found many differences between life forms and among species for the traits analyzed. Regarding traits that influence carbon dynamics in the ecosystem, grasses and shrubs had similar values for relative growth rate and differed in potential soil respiration (Fig. 1). Shrubs had 1.6 times larger potential soil respiration rates than grasses (Fig. 1), which could reflect higher organic matter accumulated underneath shrub canopies. The study of species effects revealed that relative growth rate was similar for all species except for *A. volckmanni*, which was higher (Fig. 1). *S. filaginoides* showed the highest potential soil respiration while *P. ligularis* and *S. speciosa* had the lowest, which were similar to bare soil ($5.6 \pm 0.6$ μg C·[g dry soil]$^{-1}$·d$^{-1}$). *M. spinosum*, *A. volckmanni*, and *S. humilis* fell in the middle (Fig. 1). Differences in potential soil respiration reflect differences in litter quality, nutrient availability, and/or differences in microbial species composition.

Rooting depth and plant phenology, traits that influenced water dynamics in the ecosystem, were different between life forms, with more variability among species for shrubs than for grasses (Fig. 1). A gradient existed in rooting depth from grasses to shrubs, with a more than fourfold difference between the shallowest (*S. humilis*) and the deepest (*S. filaginoides*) rooted species (Fig. 1). All grasses had perennial plant phenology with multiple leaf cohorts coexisting in the same tussock and continuous leaf production; shrub species *S. filaginoides* was semi-deciduous with a very short overlap between successive year leaves, and the other shrubs were deciduous with marked differences in the leaf time span (Fig. 1).

Plant traits that modify microclimatic conditions strongly differed among life forms. Soil thermal amplitude was higher for grasses than for shrubs (Fig. 1); a difference that was consistent among species with the exception of *A. volckmanni*, which presented an intermediate value (Fig. 1). *M. spinosum* and *S. filaginoides* have closed canopies and project a deep shadow to the soil underneath, contrasting with scattered shadows of *A. volckmanni* and grasses. The thermal amplitude of soil underneath grasses did not differ from bare soil ($10.4 \pm 1.2$°C, *t* test, $P > 0.05$).

Life forms did not differ in traits that affect ecosystem nitrogen dynamics, although species characteristics were dissimilar in many cases (Fig. 1). Soil potential net nitrification was very high underneath *A. volckmanni*, which is the only legume species studied (Fig. 1). Soil potential net ammonification differed in sign among species; soils under *S. humilis* showed net positive mineralization while the rest showed $NH_4$-N immobilization. Species differences in soil inorganic nitrogen mineralization could result from differences in litter quality accumulated underneath the canopy, species composition of the community of microorganisms, and the amount of soil organic matter accumulated under the canopy of each species. Plant preference for N form was marginally different, but was probably because of the effect of *A. volckmanni* that absorbed larger quantities of $NO_3$-N than $NH_4$-N (Fig. 1).

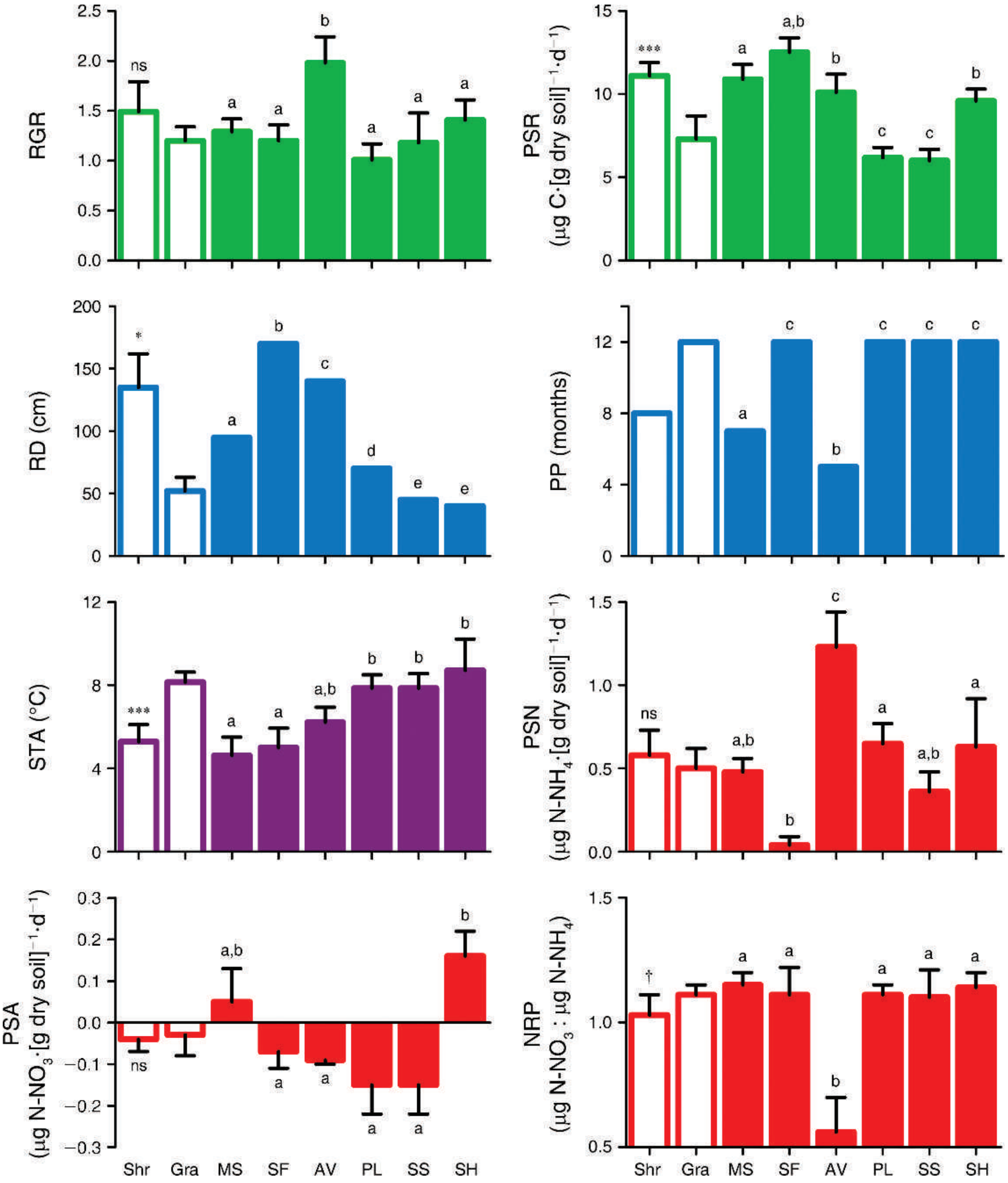

FIG. 1. Trait values related to carbon (green), water (blue), microclimate (violet), and nitrogen dynamics (red) for life forms (open bars) and plant species (solid bars) in the Patagonian steppe. Traits are: RGR, relative growth rate; PSR, potential soil respiration; RD, rooting depth; PP, plant phenology, measured as months with green leaves per year; STA, soil thermal amplitude; PSN, potential soil nitrification; PSA, potential soil ammonification; and NRP, nitrogen form relative preference. Life forms and species abbreviations are: Shr, shrubs; Gra, grasses; MS, *M. spinosum*; AV, *A. volckmanni*; SF, *S. filaginoides*; PL, *P. ligularis*; SS, *S. speciosa*; SH, *S. humilis*. Values are means + SE. Error terms are not available for RD of species because data came from previously published papers where error was calculated for horizontal rather than vertical rooting distribution. Error terms are not available for PP because all sampled individuals within a species were at the same phenological stage at each sampling date. For species, different letters above bars represent significant differences ($P < 0.05$) according to Fisher's LSD contrast. For life forms, significance was determined by ANOVA with a priori contrasts.

* $P < 0.05$; *** $P < 0.001$; † $P < 0.06$; ns, $P > 0.06$.

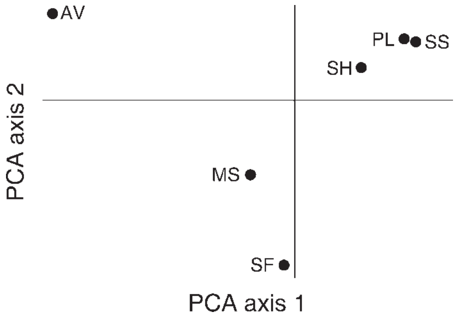

FIG. 2. Plant species ordination on the basis of species traits that affect carbon, water, nitrogen, and microclimate in the Patagonian steppe. Symbols represent species scores on the first two axes of principal components analysis. The first axis accounted for 48.2% of the variability and separated *A. volckmanni* (AV), from grasses (PL, *P. ligularis*; SS, *S. speciosa*; and SH, *S. humilis*) and the other two shrubs (MS, *M. spinosum*; and SF, *S. filaginoides*). The second axis accounted for 28.9% of the variability and separated MS and SF from the rest of the species. Trait loads are reported in Table 1A.

PCA analysis separated species according to their traits and levels (Fig. 2). The first two axes accounted for 77.1% of total variance, and separated *A. volckmanni* as the most distinctive species, from the other two shrubs, *M. spinosum* and *S. filaginoides*, and more distantly to the three grasses *P. ligularis*, *S. speciosa*, and *S. humilis*. The first axis had high loads for relative growth rates, plant phenology, and relative preference of inorganic nitrogen form (Table 1A), three traits that identified *A. volckmanni* (Fig. 1). The second axis separated the two shrubs, *M. spinosum* and *S. filaginoides*, from the rest of the species; *A. volckmanni*, which had intermediate values between grasses and shrubs for the traits on the second axis, is closer to the grasses than to the other two shrubs. The second axis had high loads for potential soil respiration, species effect on soil thermal amplitude, and species effect on potential soil nitrification (Table 1A). The third axis separated *S. humilis* from the rest of the species because of its high potential ammonification values (eigenvector = 0.84). Traits were not correlated among each other (Appendix C). The highest correlation (–0.896) was between relative growth rate and nitrogen-form preference because of the distinctive effect of one single species, *A. volckmanni*. However, no correlation was observed if *A. volckmanni* was removed suggesting that traits, in general, were not associated.

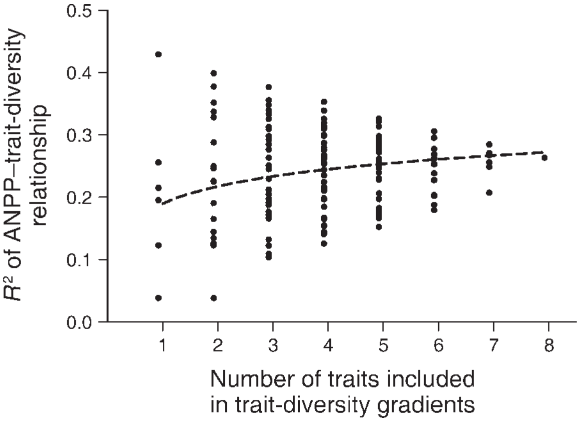

FIG. 3. Coefficient of determination ($R^2$) obtained from the relationship between aboveground net primary production (ANPP) and trait diversity in the Patagonian steppe. Each dot (255 in total) represents the $R^2$ of a regression analysis between ANPP and plant trait diversity. The $x$-axis represents the number of traits combined to generate each trait-diversity gradient. The discontinuous line represents a fitted function ($R^2 = 0.04 \ln x + 0.19$) to the number of traits included ($P < 0.001$).

### *Trait-diversity gradients*

We found a positive relationship between trait diversity and aboveground net primary production. We estimated this relationship with 255 different trait-diversity gradients and 228 presented a positive and significant relationship ($P < 0.05$, Fig. 3). The average coefficient of determination ($R^2$) increased with the number of traits, which were combined to create trait-diversity gradients ($P >> 0.001$) from 0.18 to 0.26 for one to eight combined traits (Fig. 3).

## DISCUSSION

### *How does niche complementarity occur?*

The life forms, shrubs and grasses, complement each other because they differed in water absorption patterns (Sala et al. 1989), soil thermal amplitude, and potential soil mineralization. Shrubs have deep roots and absorb

TABLE 1. (A) Trait loads for PCA reported in Fig. 2 and (B) diversity of trait values calculated with Shannon Index.

| | RGR | PSR | RD | PP | STA | PSN | PSA | NRP |
|---|---|---|---|---|---|---|---|---|
| A) Trait loads for PCA reported in Fig. 2 | | | | | | | | |
| PCA axis 1 | −0.45 | −0.29 | −0.34 | 0.46 | 0.32 | −0.31 | −0.04 | 0.43 |
| PCA axis 2 | 0.22 | −0.49 | −0.37 | −0.10 | 0.47 | 0.49 | −0.14 | −0.29 |
| B) Trait values calculated with Shannon index | | | | | | | | |
| Shannon index ($H$’) | 1.24 | 1.10 | 1.56 | 0.87 | 1.01 | 1.56 | 0.87 | 0.45 |

*Notes:* Traits are RGR, relative growth rate; PSR, potential soil respiration; RD, rooting depth; PP, plant phenology, measured as months with green leaves per year; STA, soil thermal amplitude; PSN, potential soil nitrification; PSA, potential soil ammonification; and NRP, nitrogen-form relative preference. For the Shannon index, we made values for species traits relative using a 0–1 scale and applied the Shannon modified index ($H'$) to explore which traits would have the largest contribution to niche complementarity.

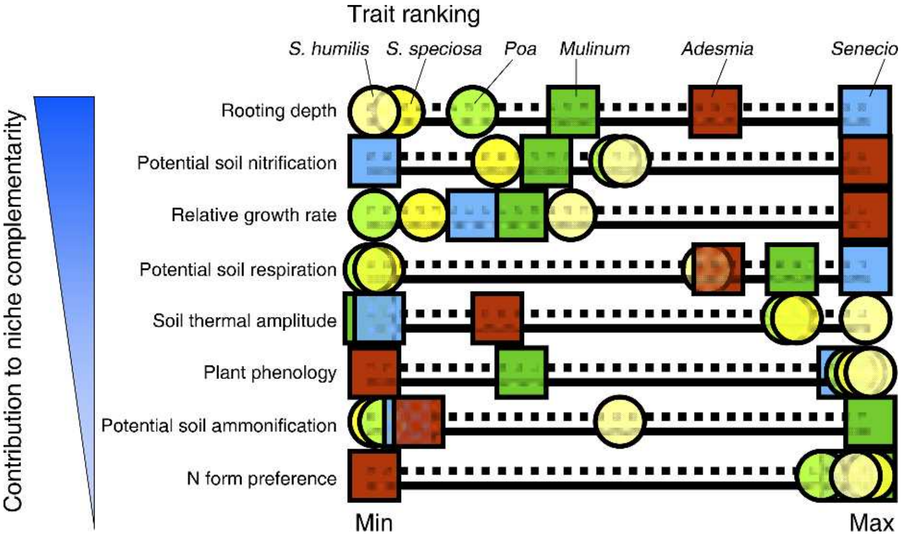

FIG. 4. Relative values of traits for all species analyzed. Each row represents a different trait, and each symbol represents a different species. Traits that were more uniformly spread across species should have a larger effect on complementarity. In contrast, traits with little variability should contribute less to niche complementarity. Here, we made each trait relative to its minimum (Min) and maximum (Max) values. Table 1B provides a quantification of species distribution for each trait.

water from deeper layers whereas grasses with their shallow roots take up water from upper soil layers. Water resources in these two layers have different seasonal dynamics and consequently shrubs and grasses are linked to two distinct resources. Deep soil layers are refilled in the winter, and this resource is utilized slowly until the middle of the growing season. Water availability in upper layers is a transient resource that could be available any time of the year. Upper layers get wet after a rainfall event and dry out fast due to the high soil evaporation characteristic of deserts. Shrubs with closed and tall canopies reduced soil thermal amplitude whereas grasses did not affect soil temperature. Also, shrub canopies concentrate production and functioned as a trap for organic matter, which resulted in 3.4 times more inorganic nitrogen (Lopez et al. 2003) and 6.7 times more carbon (Gonzalez-Polo and Austin 2009). The difference in soil organic matter between microsites located underneath shrubs and in bare soil can partially explain the observed 60% higher potential soil respiration below shrubs than below grasses.

Species in Patagonia show high degree of niche complementarity as a result of traits affecting carbon, water, microclimate, and nitrogen dynamics of the ecosystem. Grass species had similar effects on water dynamics (similar rooting depth and the same phenology) but surprisingly they differed in carbon- and nitrogen-related traits (potential soil respiration and ammonification, respectively). Within shrubs, the most distinctive species was *A. volckmanni*, a legume, with a unique effect on nitrogen dynamics (with a high potential soil nitrification and a high preference for nitrate). *A. volckmanni* also had different traits regarding carbon (high relative growth rate) and water (shortest period with green leaves), and its scattered canopy that resulted in a grass-like microclimate effect. The other shrub species, *M. spinosum* and *S. filaginoides*, differed in several traits but were less contrasted than *A. volckmanni*. Shrub species were much more heterogeneous as a group than grass species, probably because shrubs species are located in more taxonomically distant families (*M. spinosum*: Apiaceae, *S. filaginoides*: Asteraceae, *A. volckmanni*: Fabaceae) than grasses (Poaceae). The diverse phylogenetic origins characteristic of the shrub group would increase the tendency of organisms to be dissimilar (McKitrick 1993). Our findings of complementarity among species from this water-limited ecosystem are similar to the results from a nitrogen-limited ecosystem where niche complementarity among species was based on rooting depth, plant phenology, and nitrogen-form relative preference (McKane et al. 2002, Kahmen et al. 2006).

### *What are the species traits that account for most of the observed niche complementarity?*

We expected that traits with levels more uniformly spread among species would have the largest effect on niche complementarity and that, on the contrary, traits for which most of the species present the same value would have the smallest contribution to niche complementarity. We made values for species traits relative using a 0–1 scale and used the modified Shannon index ($H'$) to explore which traits would have the largest contribution to niche complementarity. Traits associated with water had the largest contribution to niche complementarity and those associated with nitrogen smallest (Fig. 4, Table 1B). Species had homogeneously spread rooting depth and potential soil nitrification

PLATE 1. Patagonian steppe, broad horizons, infinite landscapes, and rare rain showers as depicted here by the rainbow. Photo credit: O. E. Sala.

characteristics and had lumped characteristics for nitrogen-form relative preference, potential soil ammonification, and plant phenology (Fig. 4, Table 1B). There was a clear gradient for species rooting depth, a key trait in arid ecosystems since it is related to resource uptake in space and time (Golluscio and Sala 1993, Schwinning and Ehleringer 2001). Similarly, species traits were evenly distributed for potential soil nitrification; however the impact of this trait in the fitness of plant species is less direct.

### *How does trait diversity affect ecosystem functioning?*

Trait diversity increased aboveground net primary production consistently with the hypothesis that relates biodiversity and ecosystem functioning and with niche complementarity as the main causal mechanism (Vitousek and Hooper 1993, Tilman et al. 1997*b*). Complementarity is a product of species interactions and therefore combinations of traits, rather than traits of individual species in isolation. We observed an asymptotic increase in the fraction of ANPP accounted for by the number of traits along trait-diversity gradients (Fig. 3), which could be partly explained by differences in trait contribution to niche complementarity (Fig. 4), trait effects on ANPP, and correlation among traits (Fig. 2). For example, rooting depth had large effects on niche complementarity and ANPP; relative preference for nitrate or ammonia, on the contrary, had small effects.

Our results provide evidence on how niche complementarity occurs, identifies which traits had the largest contribution to niche complementarity, and shows a direct link between trait-based niche complementarity and aboveground net primary production in the Patagonian steppe.

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## SUPPLEMENTAL MATERIAL

### Appendix A

Plant species traits that affect ecosystem functioning (*Ecological Archives* E093-021-A1).

### Appendix B

Example of construction of a trait richness gradient (*Ecological Archives* E093-021-A2).

### Appendix C

Correlation coefficient among traits (*Ecological Archives* E093-021-A3).