

Grazing-induced losses of biodiversity affect the transpiration of an arid ecosystem

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Abstract Degradation processes often lead to species loss. Such losses would impact on ecosystem functioning depending on the extinction order and the functional and structural aspects of species. For the Patagonian arid steppe, we used a simulation model to study the effects of species loss on the rate and variability (i.e. stability) of transpiration as a key attribute of ecosystem functioning. We addressed (1) the differences between the overgrazing extinction order and other potential orders, and (2) the role of biomass abundance, biomass distribution, and functional diversity on the effect of species loss due to overgrazing. We considered a community composed of ten species which were assigned an order of extinction due to overgrazing based on their preference by livestock. We performed four model simulations to test for overgrazing effects through different combinations of

species loss, and reductions of biomass and functional diversity. In general, transpiration rate and variability were positively associated to species richness and remained fairly constant until half the species were lost by overgrazing. The extinction order by overgrazing was the most conservative of all possible orders. The amount of biomass was more important than functional diversity in accounting for the impacts of species richness on transpiration. Our results suggest that, to prevent Patagonian steppes from shifting to stable, low-production systems (by overgrazing), maintaining community biomass is more important than preserving species richness or species functional diversity.

Keywords Transpiration · Variability · Order of extinction · Grazing

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Introduction

Our understanding of the diversity-functioning relationship improved as the focus of studies moved from a description of biodiversity based on species number (i.e. richness) to more realistic characterizations of this attribute (i.e. functional diversity). After decades of research, evidence has accumulated on a positive relationship between diversity and both, the rate and the stability of various ecosystem processes (e.g., primary productivity, nutrient cycling, etc.) (e.g., Cottingham et al. 2001; Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2006). However, these findings have been neither widespread nor unquestionable (Reiss et al. 2009).

Recent studies highlighted that functional diversity, biomass distribution, compensation, and species extinction order may explain part of the variability observed in the diversity-functioning relationships (e.g., Wilsey and Potvin 2000; Larsen et al. 2005; Gross and Cardinale 2005; Suding

et al. 2006; Hillebrand and Matthiessen 2009; Reiss et al. 2009). Functional diversity—i.e. the value and range of the functional traits from the organisms living at an ecosystem (Díaz and Cabido 2001)—is related to ecosystem processes because species functional traits—i.e. the characteristics of an organism affecting its individual performance—drive ecosystem functioning (Hillebrand and Matthiessen 2009). However, above a certain functional diversity, the diversity-functioning relationship may saturate because of functional redundancy (i.e. different species perform the same functional role in ecosystems; Loreau 2004). Biomass distribution has been shown to correlate with ecosystem productivity (Wilsey and Potvin 2000; Mattingly et al. 2007), while its effects upon ecosystem variability have been theoretically predicted but failed to receive experimental support, possibly because of logistical problems (e.g., difficulties in maintaining evenness treatments) (Isbell et al. 2009). Compensation, the way the remaining species respond to species extinction, has also been shown to modify the diversity-functioning relationship depending on the ability of the remaining species to buffer changes in community biomass (Suding et al. 2006; Jiang 2007). Lastly, research on the diversity-functioning relationship agrees on the important role of the particular order in which species are lost from (or added to) a community (Larsen et al. 2005; Gross and Cardinale 2005). In fact, experiments that simulate non-random species loss in natural systems associated to an extinction order documented in the field have been identified as the next generation of biodiversity studies (Grime 2002; Loreau et al. 2002).

Arid and semiarid communities display high functional diversity because they comprise a wide variety of growing forms, morphologies and physiologies (Golluscio and Sala 1993; Cowling et al. 1998). Most of these communities also show a high dominance of a few species. Grazing is one of the most frequent human activities in these environments (Asner et al. 2004) which may lead to land degradation or desertification (i.e. land degradation in arid, semiarid and dry subhumid areas resulting from various factors, including climatic variations and human activities; UN 1994) (Manzano and Nívar 2000). Desertification by overgrazing is a clear case of non-random, directional species loss; the most preferred species are lost earlier from the community (Milton et al. 1994). In addition to species loss, intense desertification reduces community biomass as the remaining species cannot fully compensate for the lost biomass of the locally extinct species (von Hardenberg et al. 2001). Thus, arid and semiarid areas (i.e. drylands) offer an opportunity to sharpen our knowledge on the effects of biodiversity loss in the context of an ongoing, threatening global phenomenon.

The objective of this paper is to evaluate the response of ecosystem transpiration rate to different scenarios of species

loss in a Patagonian steppe under risk of desertification by overgrazing. We specifically address (1) the different consequences on transpiration between the particular species extinction order expected from overgrazing and other potential orders, and (2) the role of functional diversity, biomass abundance (as a proxy for biomass compensation) and biomass distribution on the effect of the overgrazing extinction order. In both cases, we were interested in the average (i.e. process rate) and the interannual variability (i.e. stability) of transpiration rate. We used transpiration as an indicator of ecosystem functioning because it is linked to water, energy and carbon exchange between the terrestrial surface and the atmosphere (Law et al. 2002). We employed a model of soil water dynamics developed for the Patagonian steppe—DINAQUA (Paruelo and Sala 1995). The use of a simulation model grants the exploration of system behavior incorporating plausible rules based on the available knowledge for an arid ecosystem.

Materials and methods

For our simulation analysis, we considered a community composed of 10 species which differed in root distribution, phenology, and water economy. Each species was assigned an order of extinction by overgrazing based on the literature and expert opinions. In one set of simulations, we modeled transpiration rate of the intact community and of all possible combination of species loss, one of which was the extinction order expected from overgrazing. Initial biomass distribution was similar to that of undisturbed communities. Total community biomass decreased as species went extinct. To break the correlation between species number and total biomass or functional diversity and to isolate the possible effect of biomass distribution from that of species traits (i.e. break the possible correlation between extinction order due to grazing and due to abundance), we performed three further sets of simulations. First, we kept biomass constant by letting the least preferred remaining grass or shrub to compensate for the biomass lost by each extinct shrub or grass/forb, respectively. Second, we held community functional diversity constant by removing proportional amounts of biomass from the 10 species instead of removing all the biomass from a single species. Third, we considered equal initial biomass distribution between species without biomass compensation and species were lost following the extinction order.

Model description

DINAQUA simulates soil evaporation, drainage, and transpiration of up to 10 species on a daily step. Model inputs are species features and daily temperature, radiation,

and precipitation. Each species is characterized by the root relative density per soil layer, the maximum and minimum green biomass (g m^{-2}), dates of beginning, end, and biomass peak of the growing season, the maximum transpiration rate, and the available water threshold (Table 1). The model simulates the seasonal course of green biomass linearly interpolating between the minimum and maximum biomass dates. The available water threshold is given by the effective soil water content—i.e. sum of the available water of each soil layer weighted by the root proportion of a given species—at which actual transpiration is reduced relative to the maximum transpiration rate. DINAQUA considers saturated water fluxes among six soil layers, and the water content of each layer is daily updated as a function of precipitation, evaporation, transpiration, the incoming flow from the upper layer and the layer's percolation. The model assumes that there is no surface runoff, and therefore precipitation is fully incorporated to the soil. Evaporation is estimated by means of the algorithm developed by Ritchie (1972). Daily transpiration from each functional type is proportional to its maximum transpiration rate per unit of green biomass (i.e. maximum transpiration), the effective soil water content and its biomass. When soil water content exceeds the available water threshold, transpiration is no longer equal to maximum transpiration and decreases linearly with soil water content

(i.e. actual transpiration). The downward water flux from the deepest layer is considered drainage. To evaluate the potential effects of facilitation on the transpiration-richness relationship, we modified DINAQUA's code to include facilitation effects based on findings reported by Aguiar and Sala (1994). These authors documented that grasses growing close to shrubs experienced an evaporative demand between 30 and 40% lower than those located at 1 m (Aguiar and Sala 1994). The facilitation sub-model incorporated to DINAQUA reduced evaporation as a function of shrubs biomass up to 64% of the evaporation initially estimated, increasing the water content from the upper soil layers where most the grasses and forbs' roots are located. DINAQUA has been successfully tested at the prediction level in the Patagonian steppe (Paruelo and Sala 1995) and in Californian grasslands (Jackson et al. 1998).

Input data

Species

The species considered were three shrubs, *Adesmia volckmanni*, *Mulinum spinosum* and *Senecio filaginoides*, two xerophytic grasses, *Poa ligularis* and *Stipa speciosa*, two mesophytic grasses, *Bromus pictus* and *Hordeum comosum*, two perennial forbs, *Adesmia lotoides* and *Callandrina*

Table 1 Parameters characterizing species rooting pattern, phenology, biomass, transpiration and soil available water as used in the soil water model simulations

Parameter	Species									
	<i>Advoc</i>	<i>Musp</i>	<i>Sefi</i>	<i>Poli</i>	<i>Stsp</i>	<i>Bropi</i>	<i>Hocom</i>	<i>Calpat</i>	<i>Adlo</i>	<i>Gila</i>
Root distribution (%)										
0–10 cm	0.011	0.036	0.252	0.468	0.518	0.51	0.508	0.815	0.689	0.815
10–20 cm	0.037	0.095	0.135	0.214	0.156	0.165	0.168	0.148	0.191	0.148
20–40 cm	0.148	0.3	0.204	0.186	0.168	0.17	0.171	0.035	0.118	0.035
40–80 cm	0.439	0.54	0.235	0.13	0.157	0.153	0.151	0	0	0
80–120 cm	0.334	0.027	0.109	0	0	0	0	0	0	0
120–200 cm	0.03	0	0.062	0	0	0	0	0	0	0
Phenology										
JD _{ini}	264	156	296	296	330	288	296	249	258	150
JD _{max}	337	360	360	356	350	344	5	348	356	329
JD _{end}	92	92	80	20	20	20	20	150	20	10
Max. biomass (g m^{-1})	4.51	7.44	8.05	11.17	39.81	4.02	1	0.057	2.064	0.229
Min. Biomass (g m^{-1})	0	0	2.658	3.989	14.22	1.434	0.359	0.02	0.737	0
Maximum transpiration ($\text{g H}_2\text{O g green biomass}^{-1}$)	18.86	7.68	11.48	10.95	7.86	8.9	9.19	13.42	12.95	7.41
Available water threshold (%)	3.8	3.8	3.8	4.8	4	8	7	11	10	10

Root distribution data were obtained from Golluscio (2005) and Soriano et al. (1987), phenology from Golluscio et al. (2005) while biomass, maximum transpiration and available water threshold values were taken from Paruelo and Sala (1995) and Paruelo (1991). The other species parameters were calculated as mentioned in the text

Advoc *A. volckmanni*, *Musp* *M. spinosum*, *Sefi* *S. filaginoides*, *Poli* *P. ligularis*, *Stsp* *S. speciosa*, *Bropi* *B. pictus*, *Hocom* *H. comosum*, *Calpat* *C. patagonica*, *Adlo* *A. lotoides*, *Gila* *G. lacinata*. *JD* indicates the Julian day corresponding to the beginning (*ini*) and end (*end*) of the growing season and to the Julian day of peak green biomass (*max*)

patagonica, and one annual forb, *Gilia lacinata*. These species are representative of the characteristic community of the Occidental district in Patagonia (Golluscio et al. 1982), except for the forbs which were chosen within each functional type based on data availability. Parameters used to characterize each species were obtained from the literature (Table 1) except for two variables, maximum transpiration rate and the available water threshold. For three species (*Stipa speciosa*, *Mulinum spinosum*, and *Poa ligularis*), these parameters were taken from the literature (Paruelo and Sala 1995), whereas for the other seven species they were inferred from the relationship between stomatic conductance—one of the most important controls of transpiration rate (e.g., Lambers et al. 1998)—and foliar nitrogen content (Schulze et al. 1994; Kelliher et al. 1995). We adjusted a linear model to the relationship between maximum transpiration rate of the three species measured by Paruelo and Sala (1995) and leaf nitrogen content (Golluscio, unpublished data). Maximum transpiration rate for the remaining seven species was then obtained from their leaf nitrogen content (Golluscio, unpublished data) and the linear model, assuming a direct relationship between stomatic conductance and transpiration rate (Lambers et al. 1998). We employed the same methodology to estimate the available water threshold assuming that both variables were linearly related. Even though the parameters determining the maximum and minimum amount of green biomass varied among simulations, we followed the values used by Paruelo and Sala (1995) as a reference. These were 56–20 g m⁻² and 20–0 g m⁻² for grasses and shrubs, respectively (pairs indicate maximum and minimum values) (Paruelo and Sala 1995). Forb biomass parameters were set to 3 and 1 g m⁻², based on the approximately 4% of the group's average cover (Golluscio et al. 1982; Fernández et al. 1991).

Climate

We used the daily temperature, precipitation and radiation data used by Paruelo and Sala (1995), a 22-year record obtained in Río Mayo (45°S, 70°W), within the Occidental district of Patagonia. Average annual precipitation was 154 mm with a standard deviation of 47.2 mm. Average annual temperature was 8.9°C ranging between 2°C (July) and 14°C (January). Radiation was obtained by Paruelo and Sala (1995) from the Smithsonian Institution (1958) assuming a relative value of 100% of incident radiation for non-rain days and 0% for rainy days because of lack of data.

Soil

DINAQUA incorporates soil parameters for layer thickness, water content at field capacity, and water content at

wilting point for each layer, as well as the initial soil water content. All simulations were initiated with the values used by Paruelo and Sala (1995) for these parameters.

Extinction order

For the Patagonian steppe, sheep grazing is the most important factor responsible for the compositional changes of the vegetation (Soriano 1956). We based the hypothetical species extinction order due to sheep overgrazing on Golluscio et al. (1999) and on observations made by the authors and Golluscio (Table 2). Golluscio et al. (1999) classified key species—defined in terms of management decisions—into five categories of animal preference from maximum (class 1) to minimum preference (class 5). They classified the forbs as class 1, the perennial grasses *B. pictus*, *H. comosum* and *P. ligularis* as class 3, *M. spinosum* (shrub) and *S. speciosa* (grass) as class 4, and *S. filaginoides* (shrub) as class 5. Although originally classified as class 2 by Golluscio et al. (1999), we assigned the legume shrub *A. volckmanni* an extinction order prior to the other spiny shrub *Mulinum spinosum* (seventh place in the extinction order; see Table 2) because of its anti-herbivore defenses (mainly spines), and its columnar structure which confers additional grazing resistance. Thus, the extinction order as a result of grazing followed these five classes with the specific order within each class defined by our best knowledge.

Simulation conditions

We performed four sets of model simulations (Table 3). The first set (objective 1) involved 1,023 individual runs as a result of all possible combinations of the 10 species representing communities comprised of 1 up to 10 species. Each model run started with total biomass and distribution similar to an ungrazed condition (Golluscio et al. 1982;

Table 2 Overgrazing extinction order determined from literature and expert opinions

Extinction order	Species	Remnant biomass (g m ⁻²)	Community functional diversity
0	–	78.3	45.3
1	<i>Adesmia lotoides</i>	76.3	42.2
2	<i>Gilia lacinata</i>	76.1	37.6
3	<i>Callandrina patagonica</i>	76	30.9
4	<i>Hordeum comosum</i>	75	29.1
5	<i>Bromus pictus</i>	71	27.5
6	<i>Poa ligularis</i>	59.8	25.3
7	<i>Adesmia volckmanni</i>	55.3	19.6
8	<i>Mulinum spinosum</i>	47.9	12.2
9	<i>Stipa speciosa</i>	8.1	7.4

Table 3 Schematic description of the simulations performed with DINAQUA

	Simulation	Species loss	Extinction order	Biomass compensated by least palatable shrub or grass	FD compensated (biomass removed equally from all sp.)	Initial biomass
^a Although no species are lost biomass was removed in amounts corresponding to the species being lost by overgrazing	1	Yes	All possible	No	No	Real
	2	Yes	Overgrazing	Yes	No	Real
	3	No	Overgrazing ^a	No	Yes	Real
	4	Yes	Overgrazing	No	No	Equal

Paruelo and Sala 1995; Table 2). The amount of each species biomass was estimated from cover data (Golluscio et al. 1982; Flombaum and Sala 2007) and a biomass/cover ratio at functional group level -peak biomass = 56, 20 and 2.35 g m⁻² for grasses, shrubs and forbs, respectively (Paruelo and Sala 1995; and ad hoc calculation for the forbs) and cover = 29, 12, and 4%, respectively (Golluscio et al. 1982). Each species cover was then multiplied by the biomass/cover ratio of its functional group. As biomass compensation was not considered the decrease in the remaining species biomass was equal to the biomass of the species lost. From the complete set of richness–transpiration relationships thus obtained, we selected the species loss sequence associated to overgrazing and compared it with the others (i.e. 1,022). This comparison was performed for transpiration and for the coefficient of variation of transpiration (calculation explained below).

In the second and third sets of DINAQUA simulations, either community biomass or functional diversity was held constant as species were lost according to the extinction order corresponding to overgrazing. In the second set, biomass remained constant because for each species lost, one of the remaining species increased its biomass by the same amount lost by the species removed. Loss of any forb or grass was compensated for by an increase of *S. speciosa*, the least-preferred herbaceous species. Loss of any shrub species was compensated for by an increase of the least-preferred shrub, *S. flaginoides*. For the case of richness equal to 1, we modeled both *Stipa* and *Senecio* monocultures. For the third set of simulations, we kept functional diversity constant by holding species number constant and proportionally removing the amount of biomass that would be lost when each species went extinct. As in the first set of model runs, initial biomass distribution and amount was similar to an ungrazed condition. Lastly, in the fourth set of simulations, initial biomass was equally distributed among species. These sets of DINAQUA runs involved 10 simulations each (30 in total).

Data analyses

Each DINAQUA run generated an output file with the amount of transpired water (mm) per year and species. Community-level mean annual transpiration was the sum

of transpiration of all species averaged across the 22-year period. The temporal variability of community transpiration was calculated for each run by means of the coefficient of variation (CV) of the community annual transpiration. As Lehman and Tilman (2000), we partitioned the standard deviation (CV's numerator) into a variance and a covariance component:

$$CV_{(n)} = \frac{\sqrt{\sum_i \text{Var}[T_i(n)] + \sum_{i \neq j} \text{Cov}[T_i(n), T_j(n)]}}{\sum_i \bar{T}_i(n)}$$

where $CV_{(n)}$ is the coefficient of variation of annual transpiration of a n -species community, $\text{Var}[T_i(n)]$ is the variance in the annual transpiration of species i in a n -species community and $\text{Cov}[T_i(n), T_j(n)]$ is the covariance between the pair of species i and j in a n species community and $\bar{T}_i(n)$ is the average annual transpiration of species i in a n -species community. This partitioning allows the identification of the mechanism responsible for the change in the temporal variability of transpiration: the overyielding effect (i.e. when mean transpiration increases), covariance effect (i.e. when species asynchrony increases) and portfolio effect [i.e. when temporal variance (σ^2) scales with the mean (m) according to the power function $\sigma^2 = cm^z$ and $z > 1$] (Taylor 1961; Doak et al. 1998; Lehman and Tilman 2000; Cottingham et al. 2001). Each component of the CV (variance, covariance and mean transpiration) was then regressed against species number to assess how these variables changed with richness. We also calculated z as the slope of the log(variance) vs. log(mean) relationship where transpiration variance and mean transpiration was calculated for each species in a community. Given the number of runs performed, we automatized the calculations of these variables using open source software (GAWK; Free Software Foundation, 2006).

Functional diversity was estimated according to the methodology proposed by Petchey and Gaston (2002), using the R routine written by Owen Petchey (R 2.4.1 Development Core Team 2006). Briefly, the total vertical distance of the vertical segments of a dendrogram branches constructed from species functional attributes—by means of Euclidean distance and the unweighted pair-group clustering method using arithmetic averages (UPGMA)—is used as a good estimator of community functional

diversity. Thus, a species loss would imply a functional diversity reduction equal to the distance of the vertical segment exclusively belonging to the lost species. This approach has many advantages compared to other functional diversity measures—e.g., functional group number—because it not only avoids the arbitrary definition of a functional difference as significant but also provides a quantitative measure of functional diversity (Petchey and Gaston 2002). The functional attributes used in the dendrogram construction are presented in Table 1, except for maximum and minimum biomass—which were not considered—and the addition of a parameter related to the maintenance of green biomass during winter. These parameters were normalized so as to be expressed in similar units.

Results

Mean annual transpiration

Mean annual transpiration varied from 47.4 mm/year (10 species community) to 0.03 mm/year (*C. patagonica* only), while mean transpiration for the 1,023 runs amounted to 28.9 mm/year. When the facilitation sub-model was not considered, mean annual transpiration decreased to 45.7 mm/year for the complete community while mean transpiration of the 1,023 runs was 28.5 mm/year. Facilitation neither modified the relationship between mean annual transpiration and richness as the correlation coefficient between mean annual transpiration with and without facilitation was 0.99 ($n = 1023$, $P < 0.0001$).

Mean annual transpiration was very sensitive to the sequence of species loss (Fig. 1). Depending on the particular

extinction order, the relationship between transpiration and richness took various forms: linear, asymptotic, exponential, or irregular. Interestingly, the overgrazing extinction order had less impact on transpiration than any other. The simulations corresponding to the overgrazing extinction order (simulation 1, Table 3) resulted in an asymptotic relationship between diversity and transpiration (Fig. 1a). The loss of the three forbs and two of the three palatable grasses had minimal consequences on transpiration. Once the third palatable grass was lost, transpiration decreased markedly. However, a community composed of the two least preferred species (*S. speciosa* and *S. flaginoides*) sustained ca. 70% of the 10-species community transpiration. Particularly, the loss of *S. speciosa* was critical.

Community biomass was more important than functional diversity in shaping the relationship between diversity and transpiration (Fig. 1b). When species loss driven by overgrazing was compensated for by increasing biomass by the least-preferred grass or shrub (simulation 2, Table 3), the resulting communities displayed higher transpiration and were largely insensitive to species loss in spite of the changes of functional diversity. Communities with constant biomass but variable functional diversity transpired on average 12 and 18% more water than communities where biomass and functional diversity changed (original extinction order) depending on whether monocultures consisted of *S. speciosa* or *S. flaginoides* respectively. In this last case, monocultures from the shrub species (*S. flaginoides*) increased transpiration compared to other communities (Fig. 1b). In contrast, when species loss driven by overgrazing was not compensated for by increasing biomass by the least-preferred grass or shrub, but functional diversity remained constant (simulation 3, Table 3), transpiration was more sensitive and closely resembled the response observed

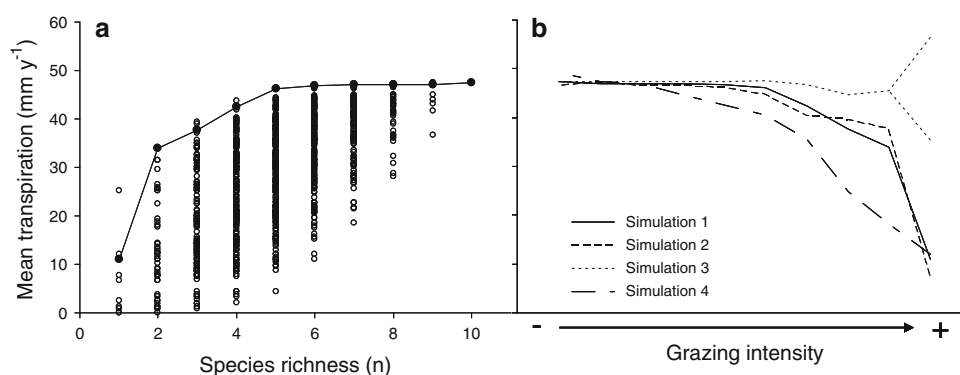


Fig. 1 **a** Mean annual transpiration rate as a function of species richness under different scenarios of extinction order. *Open circles* represent each of all possible species combinations. *Filled circles* connected by a *line* represent the overgrazing extinction order. **b** Mean annual transpiration modeled under different assumptions plotted along a grazing gradient given by the overgrazing extinction order. *Continuous line* indicates the overgrazing extinction order with

changing biomass and functional diversity (same as in **a**) included as a reference; *dashed line* the biomass varied and functional diversity remained constant; *dotted line* the biomass remained constant and functional diversity varied; and *dashed-dotted line* the initial biomass was equitatively distributed among species. The bifurcation to the *right* of the *dotted line* represents monocultures of either *S. flaginoides* (*upper*) or *S. speciosa*

for the original situation with no compensation for biomass or for functional diversity. Average transpiration from communities with constant functional diversity was almost similar (0.4% lower) to that from communities where biomass and functional diversity changed. Lastly, when equal biomass distribution among species was considered (simulation 4, Table 3), community transpiration decreased with decreasing species number in a more linear fashion than when biomass was distributed following the observed distribution in the field (linear model $r^2 = 0.88$ vs 0.60 for even and observed biomass distribution).

Interannual variation of transpiration

The interannual variation of transpiration was also very sensitive to the sequence of species loss (simulation 1, Table 3; Fig. 2a). Transpiration CV varied between 2% (*S. filaginoides* monoculture) and 17% for the complete 10-species set. The overgrazing extinction order was located towards the upper extreme of the scattered points (Fig. 2a). Thus, the extinction sequence due to overgrazing implied a minimal alteration of variability with species loss than any other extinction order. This pattern of transpiration CV and richness relationship is the outcome of a roughly matched decrease in the numerator of CV (i.e. the square root of the variance and covariance summation) and in the CV denominator (i.e. mean community transpiration) up to approximately 5 species. Thereafter, the CV numerator decreases at a higher pace than the denominator, rendering the decreasing pattern of the CV from 5 to 1 species. In particular, the three components of CV exhibited asymptotically decreasing relationships as richness decreased with total covariance showing the highest decrease rate (slopes of the linear model adjusted for each

variable were: 1.38 ($r^2 = 0.6$), 5.82 ($r^2 = 0.79$) and 2.91 ($r^2 = 0.6$) for total variance, total covariance and mean transpiration, respectively—in every case $P < 0.0001$). The variance of transpiration increased linearly ($F_{1,53} = 1,175$, $P < 0.0001$, $R^2 = 0.956$) with the logarithm of mean transpiration for each species in each plot according to the equation: $\log(\text{variance}) = -1.41 + 1.78 \log(\text{mean})$.

Biomass abundance and distribution affected transpiration variability more than functional diversity (Fig. 2b). When species loss driven by overgrazing was compensated for by increasing biomass by the least-preferred grass or shrub (simulation 2, Table 3), the resulting communities displayed higher transpiration variability and were largely insensitive to species loss in spite of the changes of functional diversity. Communities with constant biomass but variable functional diversity displayed a coefficient of variability of, on average, 20–26% higher than communities where biomass and functional diversity changed (original extinction order) depending on whether monocultures consisted on *S. speciosa* or *S. filaginoides* respectively. *S. filaginoides* monocultures were significantly more variable than *S. speciosa* monocultures (Fig. 2b). In contrast, when species loss driven by overgrazing was not compensated for by increasing biomass by the least-preferred grass or shrub, but functional diversity remained constant (simulation 3, Table 3), transpiration variability was more sensitive and closely resembled the response observed for the original situation with no compensation for biomass or for functional diversity. Average transpiration from communities with constant functional diversity was equal to that from communities where biomass and functional diversity changed. Lastly, when biomass was distributed equally among species (simulation 4, Table 3), community transpiration variability decreased with decreasing species

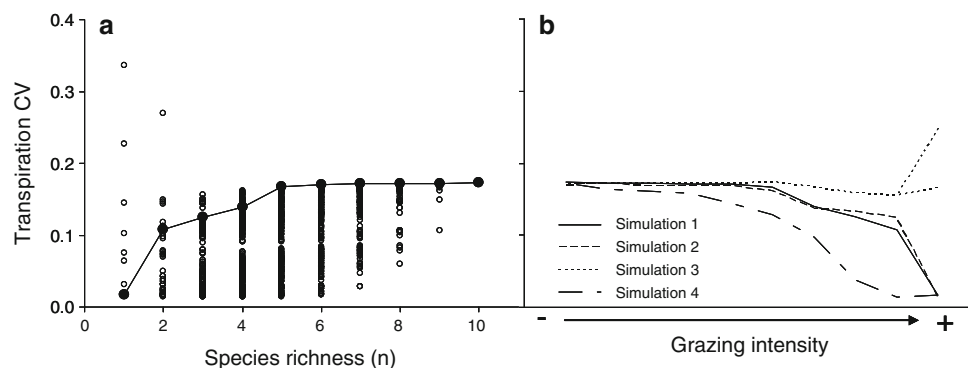


Fig. 2 **a** Interannual variation of transpiration rate as a function of species richness under different scenarios of extinction order. *Open circles* represent each of all possible species combinations. *Filled circles* connected by a *line* represent the overgrazing extinction order. **b** Interannual variation of transpiration rate modeled under different assumptions is plotted along a grazing gradient given by the overgrazing extinction order. *Continuous line* indicates the overgrazing

extinction order with changing biomass and functional diversity (same as in **a**) included as a reference; *dashed line* the biomass varied and functional diversity remained constant; *dotted line* the biomass remained constant and functional diversity varied; and *dashed-dotted line* the initial biomass was equitatively distributed among species. The bifurcation to the *right* of the *dotted line* represents monocultures of either *S. filaginoides* (*upper*) or *S. speciosa*

number in a more linear fashion than when biomass was distributed following the observed distribution in the field (linear model $r^2 = 0.88$ vs. 0.65 for even and observed biomass distribution).

Discussion

Community transpiration

The overall positive relationship between richness and water transpired found here agrees with most empirical and theoretical works (Fig. 1) (Schwartz et al. 2000). For example, from a manipulative experiment at the same area, Flombaum and Sala (2008) reported that aboveground productivity increased linearly from monocultures to communities composed of 6 species. Three causes have been put forward to explain why higher species richness may lead to increased ecological function: strong effects from a unique species (i.e. sampling effect) (Huston 1997; Tilman et al. 1997a), facilitative interaction among species (Tilman et al. 1997b; Loreau 1998), and niche differentiation (i.e. complementary effect) (Tilman 1999). In this work, the sampling effect was nil as we simulated all possible species combinations. The effect of facilitation was low compared to the same set of simulations performed without the facilitation sub-model. This result agrees with a recent study (Cipriotti, unpublished data) which suggests that the role of positive interactions in the Patagonian steppe is much lower than previously assumed (Aguiar and Sala 1994). Therefore, the positive richness–transpiration relationship must have been caused by higher resource utilization through niche differentiation as the number of species and community biomass increased.

Our modeling study of a dryland community transpiration suggests that biomass abundance and distribution appear to affect ecosystem functioning more than functional diversity. This is evident from Fig. 1 as: (1) when biomass was held constant, mean transpiration changed little as diversity declined, (2) when biomass was evenly distributed among species, there was a linear decline in mean transpiration with diversity, and (3) even after forcing functional diversity to remain constant but allowing biomass to vary with richness, mean transpiration declined similarly to the overgrazing scenario (where biomass and functional diversity varied with species number). While this result supports the “mass-ratio” hypothesis (Grime 1998)—which states that a given ecosystem process is mainly determined by the set of species that encompasses the major part of the community biomass—it also suggests the existence of a biomass threshold beyond which the loss of certain species with particular attributes impacts on ecosystem functioning. This fact is evident from the

different slopes displayed by the transpiration–richness relationship when initial biomass was equally distributed. These findings have profound implications for ecosystem management. For example, the importance of biomass destruction events such as fire or overgrazing is highlighted given that complete biomass compensation is not frequent in arid and semiarid ecosystems (e.g., Buonopane et al. 2005). Moreover, our results suggest that ecosystem management should focus on the dominant species—and not on the complete species pool—if the objective is to preserve the functioning of water limited systems because these species will provide soil cover that would control soil erosion delaying desertification progress (Schlesinger et al. 1990; Kéfi et al. 2007). On the contrary, if the objective is to increase secondary production, management decisions should focus on species with high forage value as most grazing management schemes in Patagonia do (Golluscio et al. 1998).

Figure 1 also agrees with previous findings on the critical role of extinction order on the functional consequences of diversity loss (e.g., Larsen et al. 2005). The asymptotic relationship between diversity and transpiration when extinction order was driven by overgrazing suggest that species’ effect traits (those that determine the functional contribution of a species) are negatively related to response traits (those that determine the sensitivity to disturbance) (Larsen et al. 2005). This could be the case if palatability (i.e. grazing preference) were associated to species traits that do not contribute significantly to transpiration in the Patagonian steppes. Alternatively, the documented diversity–transpiration relationship might be a consequence of an association between palatability and species abundance that may reflect evolutionary adaptations to grazing or aridity (Milchunas et al. 1988). Independently of the cause, this study showed that overgrazing-driven loss of plant species reduces community transpiration less rapidly than expected from any other extinction order and reinforces the importance of abundant, unpalatable species to narrow ecosystem disruption due to grazing.

Community transpiration variability

Results from the model simulations do not unequivocally support the hypothesis that a higher species number stabilizes communities. The only cases where transpiration variability decreased with richness were associated to the particular temporal dynamics of monocultures of *G. lacinata* or *C. patagonica*, two shallow-rooted rare herbs (Fig. 2a). In most other cases, transpiration variability increased with species richness. From the three mechanisms by which theory predicts that greater diversity leads to reduced temporal variability, we only found support for the portfolio and overyielding effect suggesting that the

observed positive relationship between variability and richness is mainly because of species asynchrony effects. Evidence for the portfolio effect comes from the observed z value of 1.8 which, as being greater than 1, implies that statistical averaging contributed to reduce transpiration variability. The overyielding effect requires that community transpiration increase with richness which it did as the 10-species community transpired 4 times more than when only *S. filaginoides* was present. However, contrary to the requirement of the species asynchrony effect, species covariance was positively associated to species number. That is, species from the Patagonian steppes generally responded in the same direction to interannual variations in water availability, a pattern also observed in other arid environments (Valone and Hoffman 2003). In Patagonia, the importance of water as a limiting factor reduces the spectrum of possible vegetation responses. Moreover, the highly predictably water availability pattern—as a consequence of winter precipitation soil water availability is high at the beginning of the growing season—additionally constrains the range of vegetation responses.

Similarly to community transpiration, transpiration variability was mainly associated to biomass (abundance and distribution) and, to a lesser extent, functional diversity (Fig. 2b). This fact reinforces the mass-ratio hypothesis (Grime 1998) and offers an explanation for the lack of response of transpiration variability to the loss of the most variable species (i.e. forbs) as these species share a small fraction of community biomass. Indeed, the extinction order modeled with equal initial biomass for every species displayed a steeper decrease in transpiration as species went extinct.

It seems pertinent to discuss to what extent our findings are influenced by the model assumptions and the parameters used to characterize species. DINAQUA does not consider soil water redistribution, establishment of new individuals, interannual variations in the seasonal course of biomass or litter. Of course, consideration of these phenomena could conceivably lead to different results than those reported here. However, we have confidence in DINAQUA because it has been successfully tested at the studied site (Paruelo and Sala 1995) and others (Jackson et al. 1998), because our findings are consistent with experimental results recently reported by Flombaum and Sala (2008) at the same site. The parameters used to characterize species may also have biased our results. Potential transpiration rate, for example, may not be a linear function of foliar nitrogen; however, this potential bias would not influence our findings because the species level extinction order was unrelated to potential transpiration rate.

Our work suggests that depauperate plant communities due to human activities that cause degradation in drylands will often exhibit lower transpiration and transpiration

variability than species-rich communities, mainly due to biomass reduction. In these systems, maintaining community biomass is more important than preserving species richness or species functional diversity to avoid the development of stable low-productive systems by overgrazing.

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