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RESEARCH ARTICLE

Stability of ecosystem functioning and diversity of grasslands at the landscape scale

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Abstract Diversity often increases ecosystem functioning and enhances stability, but this relationship has been evaluated at the community scale and considering, for the most part, only species richness. Here, we explored the relationship between landscape diversity and either the coefficient of variation or the interannual standard deviation of greenness in Pampean grasslands and Patagonian meadows, and tried to elucidate the mechanisms responsible for the resulting patterns. The coefficient of variation decreased with increasing landscape richness in Pampas but remained constant in Patagonia, while the interannual standard deviation of greenness decreased in both regions. The diversity–variability relationship in Pampean grasslands was largely accounted for by the mechanism of statistical averaging, while in Patagonian meadows, it was accounted for by a combination of statistical averaging, mean–variance rescaling and positive covariation of landscape units. There were no cases of negative covariance among landscape units. This is the first demonstration that landscape diversity increases stability of ecosystem functioning.

Keywords Richness · Equitability · Temporal variability · Ecosystem functioning · Statistical averaging · Insurance hypothesis · Primary productivity · EVI · Flooding pampa · Patagonian meadow

Introduction

Grassland ecosystem functioning, such as primary productivity and decomposition rate, changes daily, seasonally, and annually as a result of several factors. Climate is a major agent of temporal variability, largely through the occurrence of drought and flooding events (Paruelo and Lauenroth 1998; Fang et al. 2001; Knapp and Smith 2001; Goulden et al. 2004; Pennington and Collins 2007). Disturbances such as grazing and fire also control the variability of primary productivity through the removal of biomass and the alteration of nutrient cycling, among other effects (Briggs and Knapp 1995; Oesterheld et al. 1999).

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Grassland biodiversity may influence the response of ecosystem functioning to these agents of variability and, as a result, may confer stability, i.e., a relative constancy of ecosystem properties after the variation of some external agent (McCann 2000; Cottingham et al. 2001; Caldeira et al. 2005; Hooper et al. 2005; Ives and Carpenter 2007; Ebeling et al. 2008). Several studies have found that diversity enhances the stability of ecosystem functioning in the face of environmental fluctuations, disturbances or extreme events (e.g., extreme dry years) (Tilman and Downing 1994; Tilman 1996; Loreau et al. 2001; Isbell et al. 2009; van Ruijven and Berendse 2010), but others have shown neutral or inconsistent effects (McNaughton 1985; Schwartz et al. 2000; Cottingham et al. 2001; Grman et al. 2010; van Ruijven and Berendse 2010). Most of these studies used the number of species in a community as an estimator of diversity. However, the concept of biodiversity goes beyond species richness to encompass the number, abundance, and composition of genotypes, species, functional groups, and landscape units (Díaz and Cabido 2001; Tilman et al. 2001; van Tienderen et al. 2002; Diaz et al. 2006; Madritch et al. 2009). Landscape-level heterogeneity is especially relevant because most decisions about resource management and conservation are made at this scale.

Several mechanisms proposed to explain why diversity increases stability at the community scale may also act at the landscape level. The first and most frequently invoked mechanism is that species respond differentially to changing environmental conditions. Thus, in the face of stress or disturbance, the abundance and contribution to ecosystem processes may decrease in some species and increase in others, resulting in a stabilizing effect (“Insurance hypothesis”, McNaughton 1977; Naeem and Li 1997; Yachi and Loreau 1999; Ives et al. 2000; McCann 2000). This mechanism results from competitive compensation or from opposing species responses to environmental drivers (Micheli et al. 1999). Negative covariances among the interacting species can be taken as an indication of such mechanism. At the landscape scale, competition between landscape units is unlikely, but different units may have opposing responses to changing environmental conditions: for instance, within a wetland, drought may enhance lowlands productivity that would otherwise be reduced by waterlogging, and at the same time negatively affect uplands. A wet year may have opposite effects. As a result, a mixed landscape may exhibit lower interannual variability than either pure landscapes.

A second mechanism, which does not involve species interactions, is that species randomly and independently fluctuate, and hence decrease the variability of the community as a whole. This mechanism, known as “statistical averaging” or portfolio effect (Doak et al. 1998; Tilman et al. 1998; McCann 2000; Cottingham et al. 2001; Isbell et al. 2009), occurs whenever the variability of an aggregated property (i.e., variability at community scale) is computed as the sum of individual variability (i.e., variability of individual species), and a lack of covariation among the interacting species is an expected outcome (McCann 2000). Negative covariances, as in the first mechanism, strengthen the stabilizing effect of statistical averaging, while positive covariances among species, as in a case of a strong mutualism, will weaken it (Doak et al. 1998; Isbell et al. 2009). At the landscape scale, this mechanism could operate whenever the different landscape units respond independently to changing environmental conditions or disturbances. Grazing pressure, for instance, can significantly differ between landscape units depending on abiotic (e.g., slope, distance to water) and biotic factors (e.g., productivity or species composition) (Bailey et al. 1996, Adler et al. 2001), which may explain their independent fluctuations.

A third mechanism is that the response of a community as a whole is heavily influenced by the response of particular species. However, this effect of species identity (i.e., “idiosyncratic response”) (Lawton 1994; Emmerson et al. 2001; Scherer-Lorenzen et al. 2003) does not necessarily lead to a positive relationship between diversity and stability. As a matter of fact, it could result either in positive or negative slopes. At the landscape scale, this mechanism could operate when the response of a landscape to changing environmental conditions is heavily influenced by the composition of landscape units. For example, if two landscape units differ in their sensitivity to a disturbance, one being very tolerant and the other very susceptible, the response of the landscape as a whole will be heavily influenced by the relative abundance of those units.

Grassland diversity at the landscape scale can be described by the number and abundance of units or plant communities in the landscape. Each unit (from now on, "community") has a particular species composition and richness, and occupies particular portions of the landscape with common environmental characteristics. It also has a particular seasonal and inter-annual pattern of functioning and response to environmental fluctuations. Based on the same mechanisms considered at the community scale, we expect a positive relationship between landscape diversity and stability. As a result, ecosystem functioning at the landscape-level will vary less in time as landscape diversity increases. Importantly, this pattern may result from multiple factors such as negative covariances of ecosystem functioning of different communities (i.e., insurance hypothesis), statistical averaging, and the relative importance of the response of a certain community type to a given environmental fluctuation (i.e., idiosyncratic response). To our knowledge, the landscape-level relationship between diversity and stability and its underlying mechanisms have not been explored yet.

The objective of this study is to analyze the relationship between diversity and temporal variability of ecosystem functioning at the landscape scale in two study systems, and explore the relative importance of the mechanisms cited above. We used landscape richness and equitability as indicators of diversity, and the interannual coefficient of variation and the interannual standard deviation of greenness as indicators of relative and absolute temporal variability (i.e., instability of energy interception) of ecosystem functioning.

Methods

We worked in a portion of the Flooding Pampa grasslands and in a group of Patagonian meadows (Argentina). The two regions widely differ in latitude, mean annual temperature, and the seasonal distribution of rainfall (Table 1). However, they have in common a high landscape heterogeneity shaped by variations of water availability: flooded areas and small ponds alternate with well-drained areas (León et al. 1998; Perelman et al. 2001). As a consequence, they have similar physiognomy and above ground primary productivity (Table 1) (Sala et al. 1981; Paruelo et al. 2004).

We quantified the interannual variability of greenness (as an inverse indicator of stability) and the richness and equitability of thousands of landscapes in each region. The interannual standard deviation (SD) and the coefficient of variation (CV) of greenness were computed using the Enhanced Vegetation Index (EVI) based on MODIS images from July 2000 to June 2006 (Collection 4 of MOD13, Vegetation Indices product, http://lpdaac.usgs.gov/main.asp). Several studies have used remote-sensed greenness to monitor the seasonal and interannual variability of primary productivity of different ecosystems (Paruelo and Lauenroth 1995; Fang et al. 2001; Posse et al. 2005; Sims et al. 2006). EVI seems to perform relatively better than other indexes because of its lower saturation at high vegetation density and less sensitivity to background reflectance (Huete et al. 2002). EVI is correlated with leaf area index and with the fraction of photosynthetically active radiation absorbed by the canopy (Monteith 1981; Ruimy et al. 1994; Huete et al. 2002). In this paper we used EVI annual integral as a surrogate of primary productivity. In each region, we overlaid a grid of 250 × 250 m cells coincident with MODIS pixels (11085 cells that represented approximately 693 km^2 in the Pampas and 3854 cells that represented approximately 241 km^2 in Patagonian meadows) and calculated the annual mean, the interannual SD and the interannual CV of EVI for each cell. We discarded pixels in two steps: first, we identified a pixel as unacceptable based on the quality assurance (QA) provided in the MODIS product (Roy et al. 2002), and following the protocol suggested in http://tbrs.arizona.edu/cdrom/VI_QA/VI_QA_Sugg.html. Second, we discarded the pixels with mean EVI above the limits set by the 99% percentile of EVI distribution in both sites. In this way, the original data set was reduced by less than 5%. To characterize landscape richness and equitability, we used published maps of plant communities based on supervised land cover classification of LANDSAT images (Paruelo et al. 2004; Aragón and Oesterheld 2008). These maps showed the detailed distribution of five plant communities in the Pampas and eight in the Patagonian meadows (Table 1). By overlaying these maps on the MODIS grid, we estimated the number

Table 1 Description of the study systems

Study area	MAT (°C)	MAP (mm)	Seasonal index	Main community types	ANPP (kg ha^{-1} year^{-1})
Flooding pampas	13.8–15.9[a]	850–900[a]	0.89	Mesophytic meadows (MM), Humid mesophytic meadows (HMM), Humid prairies (HP), Halophytic steppes (HS), Vegetated ponds (VP)[a]	2900[b]–5320[c–e]
Patagonian meadows	6–10[f]	150–1000[g]	−0.86	Prairies (P); Grass steppes (GS), Grass shrub steppes (GSS), Shrub grass steppes (SGS), Shrub steppes (SS), Low cover grass steppes (LCGS), Scrublands (SC), Semideserts (SD)[h]	1300–4500[h]

MAT mean annual temperature; *MAP* mean annual precipitation; *ANPP* aboveground net primary productivity. Seasonality index: Pearson correlation between average seasonal temperature and monthly precipitation, 1 equals perfect phase and −1 perfect counter phase

References [a] Perelman et al. (2001); [b] Vecchio et al. (2008); [c] Sala et al. (1981); [d] León et al. (1998); [e] Oesterheld and León (1987); [f] Paruelo et al. (1998); [g] Jobbagy et al. (1995); [h] Paruelo et al. (2004)

and proportion of the communities for each cell, which allowed us to compute the landscape richness (i.e., number of communities) and equitability. We estimated equitability by the Pielou's index J (Pielou 1966), that combines the Shannon diversity index (H) and the number of entities (S):

$$J = \frac{H}{\log(S)}$$

Hence, J considers both the number and the proportion of communities. From now on, we will refer to each 250 × 250 m cell of this grid as a landscape.

Data analysis was performed in two parts. First, we tested if temporal variability was correlated with landscape diversity, and second, we tested if the relationship was most likely accounted for by the mechanisms of statistical averaging, insurance hypothesis (mainly the importance of negative covariances), or idiosyncratic response. For the relationship between temporal variability and landscape diversity, we analyzed the observed pattern by means of linear regressions between a measure of variability (either the interannual SD or the interannual CV of greenness as the dependent variables) and a measure of landscape diversity (either richness or equitability as the independent variable). Since contiguous landscapes are expected to be autocorrelated, the statistical significance of the resulting regressions could not be tested by standard procedures. For this reason, we used resampling techniques to obtain a resampled distribution of intercepts and slopes under the null hypothesis of no relationship between richness or equitability and stability (Efron and Tibshirani 1993). To do this, we shuffled the values of the independent variable (richness or equitability) and estimated the parameters of the regression 10,000 times. We then compared the resampled distribution of the estimated parameters with the observed ones.

In order to explore the role played by the three potential mechanisms described above, we (1) contrasted the observed relationship between temporal variability and landscape richness with a null model based on the assumption that this relationship was a consequence of statistical averaging (i.e., assuming no correlation between the functioning of the communities forming a landscape), (2) analyzed the matrix of covariances among all communities to detect either negative (insurance hypothesis) or positive covariances that would strengthen or weaken the stabilizing effect of statistical averaging, and (3) studied the variability of each community and its potential for shaping the response at landscape scale.

The null model that assumed statistical averaging was built and used as follows. The first step was to determine the interannual variability of each community: we calculated the mean and the interannual SD of greenness of all the landscapes formed by a single community (i.e., pure landscapes), and then we generated 1,000 temporal series of 6 years of EVI, for each community by randomly sampling from a normal distribution of annual EVI based on the observed mean and standard deviation of each community. The second step was to build "null" mixed landscapes based on the independent behaviour of each community, i.e., the independent 6-year series described above. We built mixed landscapes composed of an increasing number of communities until all the communities were included. We assumed that (1) the probability of occurrence of any given community in a landscape was independent of the occurrence of any other community, and (2) the area of a community in a landscape was proportional to its area in the region. For example, two-community landscapes were formed by all the pair-wise possible combinations of two communities, but the proportion of landscapes containing a given community and the area of each community in each landscape reflected its area in the region. Thus, a more extended community was included in more landscapes and with a greater area than a less extended community. In this way, we obtained 1,000 simulated temporal series for each possible combination of mixed landscapes for all levels of landscape richness. Finally, we evaluated if the observed interannual variability (CV or SD of greenness) was different from the variability predicted by the null model that assumed statistical averaging. As the null model actually generated a number of expected interannual CV and SD for each diversity value, we compared the observed values with the mean, and the 5 and 95% percentiles of the interannual variation expected under statistical averaging.

By analyzing the matrix of covariances among communities, we tried to infer other mechanisms in addition to statistical averaging: negative covariances would push the observed interannual variability below the predictions of statistical averaging (i.e., insurance hypothesis), whereas positive covariances would push observations above the predictions of statistical averaging. Finally, the idiosyncratic mechanism was inferred if observations differed from the predictions of statistical averaging due to the response of particular communities or to the tendency of certain communities to show positive or negative spatial association in the landscapes.

Results

The temporal variability of greenness measured as interannual CV decreased with increasing landscape richness in the Pampas (i.e., the observed slope fell within the 0.01% left percentile of the distribution of resampled slopes), and remained fairly constant in Patagonian meadows (i.e., the observed slope fell within the right 30% percentile of the distribution of resampled slopes, Fig. 1a). In the Pampas, landscapes with one community were 20% more variable than landscapes with five communities. The responses of the interannual CV of greenness resulted from the behaviour of its two components: standard deviation and mean. As landscape richness increased, the interannual standard deviation (SD) of greenness significantly decreased in the two regions (both observed slopes were within the 0.01% left percentiles of the distribution of resampled slopes, Fig. 1b). However, in the Pampas the response was accompanied by a slight increase of mean greenness, and in Patagonia by a significant decrease (Fig. 1c). Thus, in the Pampas, landscape richness was associated with lower absolute and relative variability, whereas in Patagonian meadows, landscape richness was associated with lower absolute variability only. The variability of greenness also decreased with increasing equitability (*J*) in the Pampas (Fig. 2). The rate of decrease was smoother than when richness was considered, but still the observed slope was considerably more negative (within the 0.1% left percentile) than the slopes generated by resampling. In Patagonian meadows, however, the temporal variability increased as equitability increased (the observed slope was within the 0.1% right percentile of the distribution of resampled slopes).

Three mechanisms differentially accounted for the responses of the interannual variability (measured as interannual CV) to landscape diversity. Regarding the first mechanism, statistical averaging, the observed relationship in the Pampas (Fig. 3a) was inside the 5–95% boundaries of the null model that assumed statistical averaging (covariance = 0), but it was consistently close to the upper boundary. This indicates that the decrease of variability (Fig. 1a) was largely accounted for by the mechanism of statistical averaging, but some features of the landscapes buffered the impact of this mechanism. In contrast, the observed relationship in Patagonian meadows (Fig. 3b) showed a much higher interannual variability than the one expected by statistical averaging, which indicates an even stronger effect of landscape structure counteracting this mechanism. Similar results were obtained when the variability was expressed as SD (results not shown). The second mechanism, negative covariance, was not important in the observed results. In no case were the observed results below the statistical averaging prediction, and the matrix of correlation among communities had no

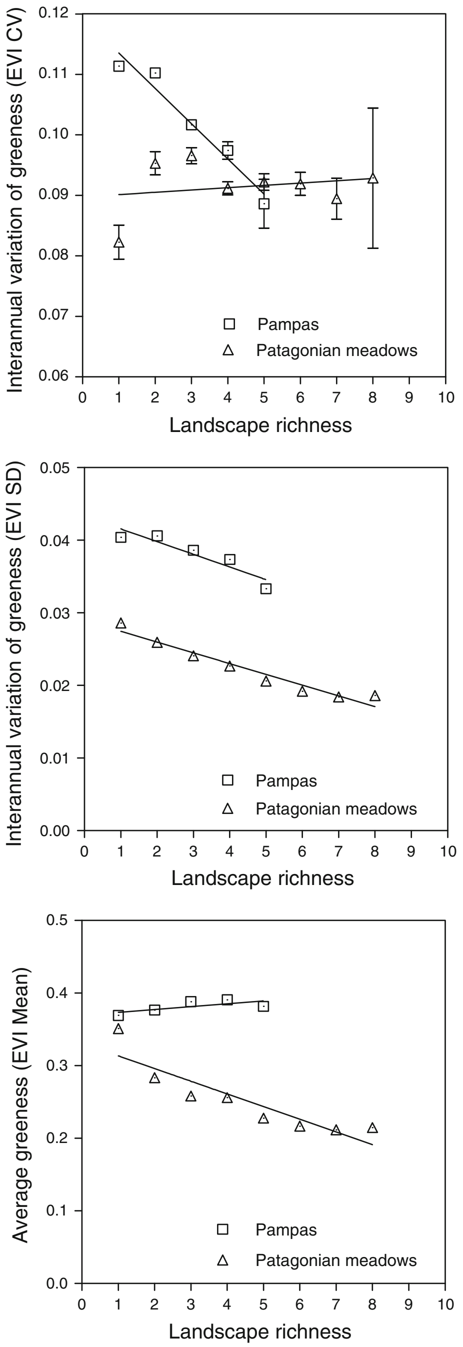


Fig. 1 Relationship between the temporal variability of greenness and landscape richness (*S*) in Pampas and Patagonian meadows. Temporal variability was estimated by the interannual coefficient of variation of greenness (EVI CV, **a**), and by the standard deviation of greenness (EVI SD, **b**). The average greenness (EVI mean) is plotted (**c**). *Error bars* correspond to standard errors (in the cases they are not visible they are smaller than the data point sizes)

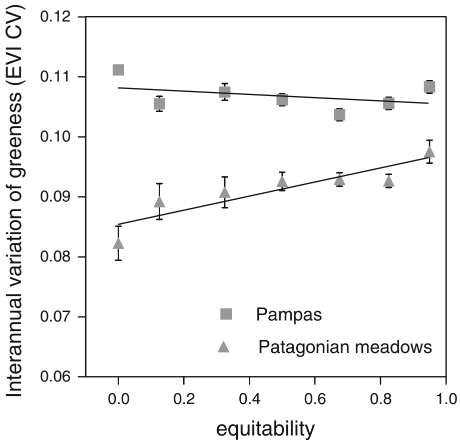
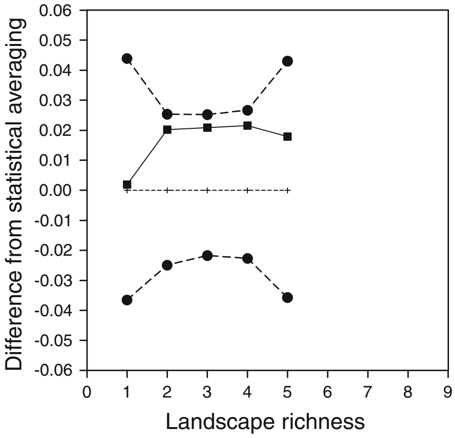


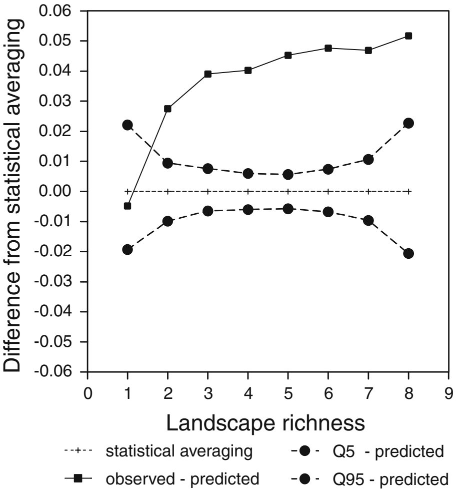
Fig. 2 Relationship between the temporal variability of greenness (EVI interannual CV) and landscape equitability (*J*) in Pampas and Patagonian meadows. *Values* on the equitability axis correspond to the mean of each of seven classes in which the original values were grouped. *Error bars* correspond to standard errors

significant negative correlations (Table 2). In fact, the matrix of correlation was consistent with the mechanism of statistical averaging counteracted by some positive correlations between some communities. In the Pampas, landscapes with two communities were most frequently formed by Vegetated Ponds and Humid Prairies, whose dynamics of greenness was uncorrelated (Table 2a). As a consequence, as richness increased (i.e., from $S = 1$ to $S = 2$) landscapes were enriched in communities whose dynamics of greenness was asynchronous, i.e., behaved as the statistical averaging model. The other communities were weakly but positively correlated, which resulted in the pattern of Fig. 1a close to the upper boundary of the area expected under the null model. In contrast, in Patagonian meadows the dynamics of greenness of the four most abundant communities was highly and positively correlated (Table 2b). As a consequence, increasing landscape richness most often meant adding communities whose temporal variability in functioning was coupled and overrode the effect of statistical averaging (Fig. 3b).

Lastly, regarding the third mechanism of idiosyncratic response, in the Pampas, the two most extended communities (Vegetated Ponds and Humid Prairies) were also the most variable (Fig. 4a). Additional communities (i.e., Mesophytic Meadows or Halophytic Steppes) were less variable, and as a



(a) Pampas



(b) Patagonian meadows

Fig. 3 Departure from the mechanism of statistical averaging for the observed relationship between the interannual coefficient of variation of greenness (EVI CV) and landscape richness (*S*) in Pampas (**a**) and Patagonian meadows (**b**). *Squares* correspond to the difference between the observed CV (as in Fig. 1a) and the CV expected under the null model of statistical averaging (mean of 1000 runs). Dashed lines indicate the limits set by the 5 and 95% percentiles of the null model (each circle corresponds to the difference between the values of the percentiles and the mean expected under statistical averaging)

consequence, landscapes with increasing richness had lower variability. On the contrary, in Patagonian meadows, the whole area was more evenly distributed among communities than in the Pampas, and two of the most abundant communities (Prairies and Grass Shrub Steppes) had intermediate variability (Fig. 4b). Thus, adding more communities neither decreased nor increased the variability at the landscape scale on average. In Patagonian meadows identity and positive covariance effects were even more marked when *J* was used as an estimator of diversity. While Prairies were over-represented in the first equitability interval, Scrublands (i.e., the most variable community) were common at higher *J* values, which explain the low and high temporal variability respectively.

A particular case of the identity effect is the pattern of association of communities in mixed landscapes. In the Pampas, the composition of the landscapes formed by two communities ($S = 2$) was far from the composition expected from random combinations according to their individual abundance ($\chi^2 = 990$, $P < 0.01$). Certain combinations showed positive associations (e.g., Humid Prairies and Humid Mesophytic Meadows) while others were highly unlikely (e.g., Mesophytic Meadows and Vegetated Ponds). If all the combinations had been equally probable, we would have expected a stronger decrease in CV when moving from $S = 1$ to $S = 2$ landscapes given the covariance structure among communities (i.e., Humid Prairies and Humid Mesophytic Meadows were positively correlated, while Mesophytic Meadows and Vegetated Ponds were not). Therefore, the identity and abundance of the different communities and their combinations in the whole region affected the relationship between variability and diversity. In Patagonian meadows, pure landscapes ($S = 1$) were dominated by Prairies, while the combination Prairies–Scrubland was one of the most common landscapes with two communities. As Scrublands were the most variable community, this may explain the increase of variability between $S = 1$ and $S = 2$ (Fig. 1a). Therefore, the lack of independence in the co-occurrence of communities in mixed landscapes was an important aspect of the effect of identity on landscape stability.

Discussion

Our results show that landscape diversity affects the interannual variability of ecosystem functioning. Specifically, we found that the relative variability of greenness decreases with increasing landscape richness in Pampas, but shows no such a trend in Patagonian meadows; while the interannual standard deviation of greenness decreases with increasing landscape richness in both study systems. Hence, the

Table 2 Spearman *r* coefficients (below the diagonal) and associated *P*-values (above the diagonal) of the dynamics of greenness (EVI annual mean) in the different communities

	HP	VP	HMM	MM	HS
a-Pampas					
HP	1	0.85	0.08	0.05	0.28
VP	0.09	1	0.57	0.34	0.08
HMM	0.77	–0.26	1	0.34	0.75
MM	**0.89**	0.43	0.43	1	0.11
HS	0.49	0.77	0.14	0.71	1

	P	GSS	GS	SC	LCGS	SD	SGS	SS
b-Patagonian meadows								
P	1	0.03	0.08	0.04	0.08	0.05	0.05	0.05
GSS	**0.99**	1	0.08	0.94	0.77	0.89	0.05	0.05
GS	0.77	0.77	1	0.71	0.31	0.43	0.34	0.34
SC	**0.94**	0.04	0.11	1	0.18	0.08	0.08	0.08
LCGS	0.77	0.08	0.48	0.6	1	0.94	0.04	0.04
SD	**0.89**	0.05	0.34	0.77	0.04	1	0.03	0.03
SGS	**0.89**	**0.89**	0.43	0.77	**0.94**	**0.99**	1	0.03
SS	**0.89**	**0.89**	0.43	0.77	**0.94**	**0.99**	**0.99**	1

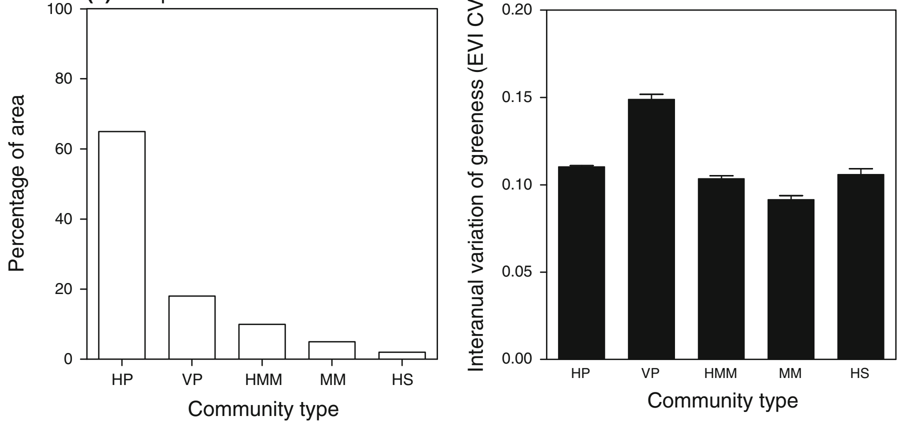
In *bold*, values significant at $P < 0.05$. Abbreviations as in Table 1

diversity–stability relationship cited at the community scale held at the landscape scale, both considering absolute or relative variability in Pampas, and only with absolute variability in Patagonia. Finding that richness of landscape units affects ecosystem temporal stability is especially relevant given that landscape homogenization is one of the main consequences of global change (Western 2001; Hietala-Koivu et al. 2004), and that several management decisions are taken within stakeholder properties, that usually represent a landscape scale.

As stated above, in Pampas, we found the same relationship between diversity and stability when we used either the coefficient of variation or the standard deviation in greenness. In Patagonian meadows, however, both estimators of variability showed different results, as the interannual CV remained fairly constant along the landscape richness gradient. There are several ways to estimate stability, such as temporal standard deviation (of crude or log-transformed data), coefficient of variation, deviance from pre-disturbed conditions (i.e., resistance) and the ability to return to undisturbed stage (resilience), among others (McGrady-Steed et al. 1997; McCann 2000; Cottingham et al. 2001). All of them have different limitations and advantages. The variability relative to the mean (CV) is one of the most widely used measures given that it does not require the identification of pre and post disturbed conditions, and that it facilitates comparisons when there is a trend in the mean values (Cottingham et al. 2001). Our results indicate that the variable chosen to quantify stability has to be taken into account when interpreting the stability–diversity relationship (McCann 2000; Cottingham et al. 2001). Importantly, in order to interpret CV results, it is advisable to consider the two parts of the quotient and how they change along the landscape richness gradient.

Mean–variance rescaling, together with statistical averaging, is often cited as a statistical mechanism that influences diversity–stability relationship (Tilman et al. 1998; Tilman 1999; Cottingham et al. 2001). This mechanism refers to the way variance scales with the mean (as a power function with a scaling coefficient z), and implies that changes in the mean along the richness gradient would inevitably affect the absolute variability. The CV or the SD of the log transformed data control for mean–variance rescaling only if $z = 2$ (Tilman 1999; Cottingham et al. 2001). Since in many studies at community scale community mean biomass increases with species richness and $1 < z < 2$, a reduction in the relative variability with diversity is an expected outcome (Tilman 1999). In Patagonian meadows, EVI mean decreases with landscape richness, tendency that is also followed by EVI SD, and

(a) Pampas



(b) Patagonian Meadows

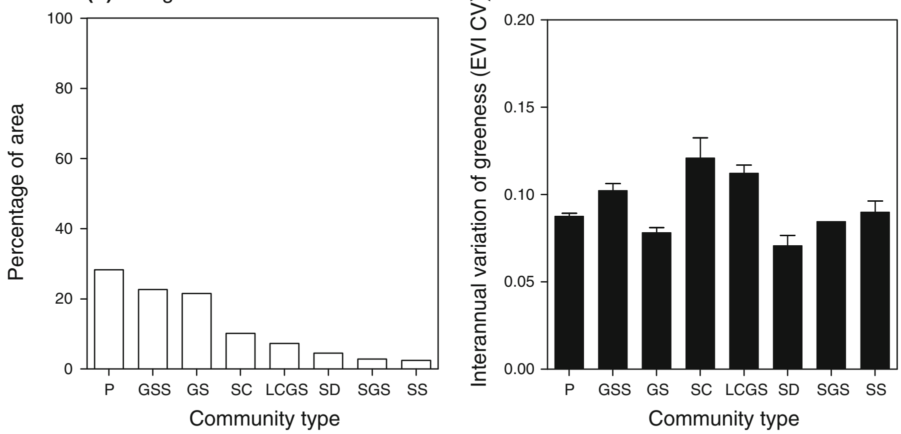


Fig. 4 Percentage of the study area (*left*), and interannual variation of greenness (EVI CV, *right*) of landscapes dominated by each community type. **a** Pampas, **b** Patagonian meadows. *Error bars* indicate standard errors. *Abbreviations* of community types as in Table 1

consequently the CV remains stable. This mean–SD dependency may be accounted for by mean–variance rescaling. However, it is important to remark that, unlike in other studies, there was a negative trend in the mean, and therefore we could not expect a reduction in CV along the richness gradient. Mean–variance rescaling does not seem to explain the diversity–stability relationship in Pampas, since the mean has a slightly increase and the SD a significant decrease along the landscape richness gradient.

The relative importance of the mechanisms that accounted for the diversity–stability relationship differed in the two study systems. The statistical averaging seems to be more important in shaping this relationship in Pampa grasslands, while the positive covariances, idiosyncratic responses and mean–variance rescaling (discussed above) seem to be critical in Patagonian meadows. The statistical averaging and the negative covariance effect are both primarily based on the concept of temporal asynchronicity of species or, in our case, asynchronicity of community responses (Yachi and Loreau 1999; McCann 2000; Cottingham et al. 2001; Grman et al. 2010). In statistical averaging, asynchronicity stems from the independent behaviour of each community of the landscape, whereas in negative covariance it stems from the opposite behaviour of each community. In Pampa grasslands and Patagonian meadows community greenness dynamics were either uncorrelated (statistical averaging) or positively correlated (stabilizing effect of statistical averaging mitigated). We found no significant negative correlation consistent with the negative covariance effect. This means that given an environmental perturbation (e.g., drought or flooding), a decrease of greenness in a community was not compensated by increases in any other. Interestingly, some communities, particularly in the Pampas, were quite independent from each other so that good years for some communities were neither good nor bad for others. However, positive associations in greenness dynamics were dominant. In the Pampas, they explain why the observed variability was very close to the upper limit of variation predicted by statistical averaging, whereas in Patagonia they offset most of the stabilizing effect of statistical averaging. It is important to highlight that even with positive correlations, the statistical averaging model successfully explained the diversity–stability relationship in the Pampas. This means that the zero covariance is not a strong requisite for this effect to manifest (McCann 2000).

There are two important differences between the two studied regions that may shape the response of their temporal variability to landscape diversity. The first difference relates to the phenological synchrony among communities in each region. On the one hand, Pampean communities include winter and summer species in different proportions, which cause a relatively broad variation of greenness dynamics among communities. For instance, halophytic steppes are dominated by C4 grasses and showed an extended peak of EVI during the summer, while mesophytic meadows are dominated by C3 grasses and have a bimodal curve with an earlier peak at the beginning of the spring (Aragón and Oesterheld 2008). This phenological displacement may be responsible for the degree of independent behaviour of some of these communities. On the other hand, Patagonian meadows are strongly constrained by environmental factors that determine a very short growing season (Jobbagy et al. 2002; Paruelo et al. 2004). As a result, all their communities have very similar seasonal patterns. Consequently, independently of landscape richness or composition, the temporal variability of different communities is coupled. As found at community level (Díaz and Cabido 2001; Loreau 1998; Yachi and Loreau 1999), the underlying functional range and the degree or overlap in community responses (redundancy) influences the stability–diversity relationship at the landscape scale. Because of this, we would expect the strength of the diversity–stability relationship to decrease along a latitudinal gradient (i.e., at high latitude the environmental factors more strongly constraint community responses).

Secondly, even though the two study systems are highly influenced by their water dynamics, in Patagonian meadows temperature significantly controls the start and length of the growing season (Jobbagy et al. 2002). Both variables are expected to show spatial autocorrelation, but water dynamics is more directional (moving from uplands to lowlands) than temperature. In the Pampas, humid mesophytic meadows can use the excess of water of a nearby mesophytic meadow (located higher in the topographic gradient) during a dry year, and therefore the spatial arrangement of landscape units is expected to be more relevant than in Patagonia. In Patagonian meadows, the movement of water is also important, but in addition, the movement of air masses that set surface temperature becomes relevant as well. Lower landscape units are wetter but at the same time cooler, and therefore this can homogenize their functioning at the landscape scale. Hence, the spatial arrangement of landscape units would play a minor role. The difference in the redistribution of the resources and control variables at the landscape scale can also be important in explaining the effect of diversity on temporal variability of greenness.

Our results depend on the spatial scale considered. The grain and extent of our landscapes were constrained by the remote sensing information we used and the vegetation surveys available. Considering much larger or smaller landscapes may have compromised the range of landscape richness to be evaluated (i.e., larger landscapes would have included most communities and smaller landscapes would have included just one or very few communities).

Previous studies have found a positive relationship between species richness and temporal stability in ecosystem function (Naeem and Li 1997; Tilman et al. 2006; Isbell et al. 2009). Our study reveals, for the first time, that the temporal stability of ecosystem function at the landscape level is also affected by landscape diversity. However, the strength of the relationship differed between the two study systems, since the pattern was more apparent in Pampa grasslands (with a decrease in relative and absolute variability) than in Patagonian meadows. Importantly, even though the same mechanisms can be used to explain the results in both study systems, their relative importance varied. Statistical averaging greatly accounted for the diversity–stability relationship in Pampas, while in Patagonian meadows the positive covariation in community functioning combined with the identity and abundance of different communities and their combinations were important as well. The differential degree of temporal asynchronicity in community responses and the relative importance of the spatial redistribution of control variables seem to be key ecological aspects in explaining the distinct patterns.

Finally, our work highlights that remote sensing techniques and modelling represent a very useful combination of tools to explore the diversity–stability linkage at landscape scale. Free-access images can provide up-to-date and frequent monitoring of ecosystem functioning (i.e., greenness dynamics), and high-resolution images can help improving landscape description. In future studies, modelling can be used to further explore how different degrees of correlation among community temporal dynamics of greenness, and changes in their relative abundance can revert the effect of statistical averaging.

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