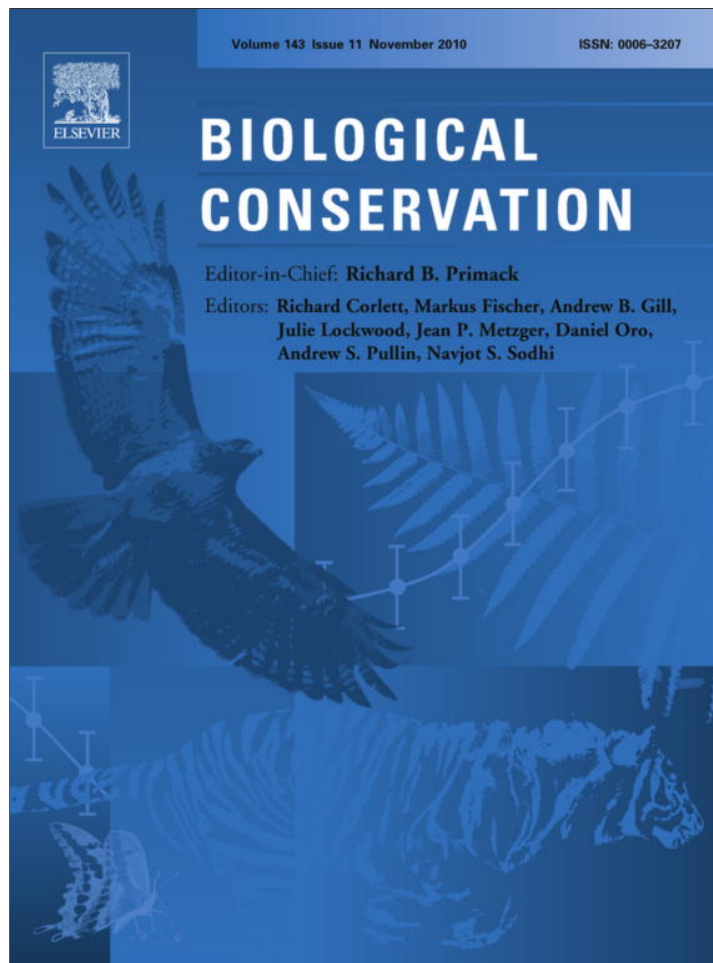


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Predicting alpha, beta and gamma plant diversity from physiognomic and physical indicators as a tool for ecosystem monitoring

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ABSTRACT

We searched for predictive models for alpha, beta and gamma plant diversity based in easy to measure field indicators. The study was conducted on the upper belt of the Córdoba mountains (Argentina). We established 222 permanent plots of 4×4 m distributed on sites with different physiognomy, topography and management. At each plot we measured physical and physiognomic indicators and recorded the presence of all vascular plants. We estimated alpha diversity as the number of species detected in a plot, beta diversity as the floristic dissimilarity between two plots, and gamma diversity as the number of species detected in a landscape. Through linear regression we found predictive models for alpha and pairwise beta diversity. Then we analysed if predicted average alpha and beta diversity were good estimators of gamma diversity. We recorded a total of 288 species (5–74 species per plot). Alpha diversity was highest in sites on shallow soils with high structural richness (i.e. high number of cover categories), half covered by lawns, at sunny slopes and rough landscapes ($r^2 = 0.66$). For beta diversity, the difference between plots in structural richness and in cover of thick tussocks grasses and lawns were the best predictors ($r^2 = 0.45$). For different sets of simulated landscapes, gamma diversity was well explained by predicted average alpha and beta diversity, plus the sampling effort ($r^2 = 0.92$). We concluded that using easy to measure field indicators it is possible to estimate plant diversity at different levels with a good accuracy.

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1. Introduction

Biodiversity losses are an increasing threat for ecosystems and the services we obtain from them (Millennium Ecosystem Assessment, 2005). Implementing management strategies aiming at biodiversity conservation is an urgent need, and an important goal of conservation agencies (Pereira and Cooper, 2006; Klimek et al., 2007; Henry et al., 2008). In this scenario, monitoring biodiversity behaviour under different management schemes becomes of vital importance, both for protected areas and for other ecosystems subjected to conservation goals (Critchley et al., 2003; Baillie et al., 2008; Henry et al., 2008).

Plants are often used as indicators for whole ecosystem diversity because they are sensitive to abiotic environment and are the primary target of most land-use pressures (Landsberg and Crowley, 2004; Lughadha et al., 2005). Also, plants are the basis of food webs, constitute the habitat of animals, and their spatial distribution influences animal diversity (Noss, 1990; Fuhlendorf and Engle, 2001; Cingolani et al., 2008a). Given the importance of

plants, monitoring vegetation at different spatial scales is necessary to implement sound and comprehensive management strategies. Plant richness is a recognized indicator of biodiversity, both at the local or regional scale, and its maximization is often a goal in itself (Gotelli and Colwell, 2001; Rocchini et al., 2005; Pereira and Cooper, 2006). The taxonomic richness of a whole region, portion of landscape, or management unit (hereafter “landscape”) has been termed gamma diversity, and can be partitioned into two components (Whittaker, 1972; Vellend, 2001; Melo et al., 2009). One of them, alpha diversity, can be defined as the number of species present at a single site or sampling plot. The other, beta diversity, can be defined as the variation in species composition among sites. For monitoring goals, it is important to consider plant taxonomic richness at these three levels, because each of them can reflect different aspects of ecosystem complexity (Cingolani et al., 2008a). However, estimating taxonomic richness is time-consuming, and often material resources and experts trained in species identification are scarce (Kati et al., 2004; Holck, 2008).

To deal with these difficulties, conservation ecologists have attempted to find variables that are easier to measure and also highly associated with taxonomic richness, for plants as well as for other organisms (Jonsson and Jonsell, 1999; Kati et al., 2004). Sometimes, selected taxa were used as indicators of other taxa which are more difficult to identify and/or measure (Kati et al., 2004; Schmidt et al.,

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2007). This approach has shown good results for gamma diversity, but was less successful for alpha diversity, because richness patterns of different taxa are seldom congruent at the site scale (Faith and Walker, 1996; Dauber et al., 2003; Kati et al., 2004). Another promising approach is to combine physical and biological indicators obtained from GIS and satellite images, to predict gamma diversity for different portions of the landscape (e.g. Lobo et al., 2001; Dumortier et al., 2002). A similar combination, but using mostly fine-resolution field indicators, can be used to predict and monitor plant alpha and beta diversity. Reported associations of physiognomy with alpha diversity and botanic composition (Collantes et al., 1999; Jauffret and Lavorel, 2003), suggest that physiognomical parameters (e.g. cover of different growth-forms) and their variation among sites could be good biological predictors of alpha and beta diversity respectively. The advantage of such structural variables is that they are relatively easy to estimate in the field, and besides their potential as taxonomic richness predictors, they can also be good indicators of ecosystem functional properties (Díaz and Cabido, 1997).

We aimed to explore this approach for the upper altitudinal belt of the Córdoba mountains, in central Argentina. This is a key area in the region because about three million people depend directly on these mountains for their water supply. Alarming soil erosion processes and loss of woodlands in the area were produced by four centuries of domestic grazing and associated fires (Cingolani et al., 2008b). To ameliorate these problems and to protect the rich endemic flora and fauna of the region, in 1997 lands were expropriated to create a National Park, and in 1999 a buffer Provincial Water Reserve was created, which remained under private ownership. When livestock was excluded after the creation of the Park, plant diversity began to decrease because highly competitive tussock grasses advanced over more diverse short grasslands previously maintained by livestock and fire (Cingolani et al., 2003). To revert these trends, livestock was re-introduced in some areas of the Park.

As part of a more comprehensive monitoring program, we are evaluating soil erosion and vegetation (both botanic composition and structural characteristics) in the Park and surrounding Reserve (Cabido, 2008). From these data, we aimed to generate a tool for rapid evaluation of diversity changes without the need of experts, to be used by government staff or local people (Danielsen et al., 2008). Because previous studies in this area reported associations of physiognomy and physical environment with plant richness and botanic composition (Cabido, 1985; Cingolani et al., 2003; Enrico et al., 2004), we explored the use of these variables as predictors of diversity. Specifically, our objectives were to: (1) find a predictive model of alpha diversity based on easy to measure physical and physiognomic variables, (2) find a predictive model of beta diversity based in the variability among sites in the same variables, (3) explore the potential of both models to produce, by combination, an estimator of gamma diversity.

2. Materials and methods

2.1. Study area

The Quebrada del Condorito National Park and the surrounding Provincial Water Reserve are located in the upper belt of the Córdoba mountains (North–South range; 1700–2800 m a.s.l.). Mean temperature of the coldest and warmest months are 5.0 and 11.4 °C respectively, with no frost-free period. Mean annual precipitation is 924 mm, with most rainfall concentrated in the warmer months, from October to April (Cabido, 1985; Colladon, 2008). The landscape consists of a mosaic of woodlands, grasslands and rocky outcrops and pavements. Woodlands are generally small

patches dominated by *Polylepis australis* Bitter. Grasslands can be dominated by tussock grasses (*Poa stueckertii* (Hack.) Parodi, *Deyeuxia hieronymi* (Hack.) Türpe and *Festuca* spp.), or by short graminoids and forbs (“grazing lawns” sensu McNaughton, 1984). Rocky outcrops have variable levels of plant cover, including all life-forms, while erosion pavements are always scarcely vegetated (Cingolani et al., 2004). Most of the species within the local flora are characteristic of this upper mountain belts and a good number of endemic species is likely to be found in both grassland and woodland communities (Cabido, 2008). In the National Park, different grazing management schemes have been implemented, involving different stocking rates and timings of grazing. In the surrounding Reserve area, stocking rates are generally higher and fire is often used to reduce tussock cover and stimulate regrowth.

2.2. Field sampling

We established 222 permanent plots of 4 × 4 m distributed in a large portion of the area, occupying a range of 50 km in the North–South direction (from 31° 23′ 15″S to 31° 46′ 33″S), and about 20 km in the East–West direction (from 64° 41′ 22″W to 64° 51′ 34″W). In altitude, the study area ranged from 1800 m a.s.l. to 2300 m a.s.l. Of these plots, 173 were located within the National Park, and 49 were in the surrounding Reserve. Plots were distributed in paddocks (or grazing areas limited by natural boundaries) under variable grazing regimes and stocking rates, which include grazing exclusion (41 plots), light to moderate grazing (112 plots), and heavy grazing (69 plots). Plots were representative of the different plant cover units and topographic conditions present in the paddocks, except that we did not sample closed woodlands (i.e. more than 50% tree cover). The size of the plots was a trade-off between including as many species as possible and allowing reasonably accurate rapid visual estimations of indicator variables.

The plots were established and measured for the first time in different years (142 in 2004, 40 in 2005, 18 in 2006, and 22 in 2008), always in September to standardize the estimation of the biological indicator variables at the driest period of the year. When setting up the plots we measured slope aspect (degrees from the north), slope inclination (%), and soil depth (cm). Soil depth was measured at each corner of the plot unless bare rock was encountered in which case we selected the nearest area with soil within the plot. The four measures were later averaged to obtain one value per plot. Location and altitude (m a.s.l.) were measured with a Global Positioning System. Within each plot, we estimated the cover (%) of bare soil and of bare rock in three categories (pavements, loose rocks, and outcrops, following Cingolani et al., 2004). We also estimated the cover of lichens (not considering those on rocks), mosses and litter, and the following vascular plant growth-forms: tussock grasses with thick leaves (mainly *P. stueckertii*, hereafter “thick tussock grasses”), tussock grasses with thin leaves (mainly *D. hieronymi* and *Festuca* spp, hereafter “thin tussock grasses”), short forbs, tall forbs (mainly sufruticose species and one vine), perennial graminoids, annual graminoids, cacti, ferns, shrubs, and trees. In all cases, cover was visually estimated in 5% categories (10%, 15%, 20%, etc.) except for low cover values (<10%), which were estimated in 1% categories (1%, 2%, etc.). When cover was far less than 1%, we registered 0.1%. In the summer (January and February) after setting up the plots we recorded the presence of all vascular plants. This date was selected because only at this season are species fully identifiable.

2.3. Data analyses

2.3.1. Variables used in the analyses

To find a predictive model for alpha diversity we used the physical and physiognomic predictor variables measured in the plots or

Table 1
Variables considered for predicting alpha and beta diversity, and their range of variation in our data set.

	Range	
	Lower	Upper
<i>Physical variables</i>		
Altitude (m a.s.l.)	1848	2274
Slope (%)	0	55
Soil depth (cm)	1.25	110
Local insolation (index)	−4.6	7.4
Landscape roughness (index) ^a	0.0058	0.1259
Landscape topographic position (index) ^a	0	100
<i>Physiognomic variables</i>		
Structural richness	1	14
Thick tussock grass cover (%) ^b	0.1	100
Thin tussock grass cover (%)	0	97
Lawn cover (%) ^c	0	105
Woody cover (%) ^d	0	62
Bare surface (%) ^e	0	52
Rock exposed by erosion (%) ^f	0	78
Outcrops (%)	0	50

^a Obtained from a Geographic Information System Cingolani et al. (2008b).

^b Thick tussock grasses + litter.

^c Annual grasses + short perennial grasses + short dicots.

^d Trees + shrubs + cacti + tall sufruticose forbs.

^e Bare soil + lichens + mosses.

^f Pavements + loose rocks.

calculated from plot measures, together with two variables obtained from a Geographic Information System (Cingolani et al., 2008b). All the variables are listed in Table 1. For beta diversity, we used between-plot differences of the same physical and physiognomic variables, plus geographical distance between plots, which is generally associated with botanic dissimilarity (Vellend, 2001). The index of local insolation (Table 1) was calculated as the cosine of the aspect multiplied by the square root of the slope inclination. In this way north facing slopes (i.e. sunnier) had positive values, grading towards negative values at south facing slopes (this surrogate does not consider projected shadows). The structural richness (Table 1) was the total number of growth-forms and other cover categories estimated in the plot, with a maximum possible of 16 (trees, shrubs, thick tussock grasses, thin tussock grasses, ferns, cacti, tall forbs, short forbs, perennial short graminoids, annual short graminoids, mosses, lichens, loose rocks, pavements, outcrops and bare soil). Cover variables were reduced to seven (by merging some cover categories on the basis of structural similarity and co-variation along plots) to avoid variables with too many zeros (details in Table 1).

2.3.2. Alpha diversity

To obtain the predictive model for alpha diversity (defined as the number of species recorded in a plot) we used multiple regression analysis, with the indicator variables listed in Table 1 as predictors. To avoid over-fitting, and allow model validation without losing valuable information for parameter calculation, we used a jackknifing procedure as explained below.

First, we produced five data-sets, each one with 80% of the plots. The discarded 20% of the plots were selected at random for each data set, but with the restriction that each of the 222 plots were discarded once.

Second, we selected only one group of predictor variables which proved the best for all the five data-sets on average. To select this group, we performed a manual forward stepwise multiple regression for each data set. When including a variable, we decided between a linear, logarithmic (or square root for variables with zeros) or a quadratic unimodal relationship, according to the r^2 obtained by the different alternatives, and the visual analysis of the scatter-plots. In this way we obtained five different alternative

multiple regression models, with very similar but not exactly the same predictor variables or terms. Then, we tested the different alternative group of variables/terms for the five data-sets with multiple regressions, and selected the group which produced the best average r^2 , and whose variables/terms were always significant and not strongly correlated among them. In this way we obtained five regression models differing only in the variables' coefficients.

Third, we used each model to calculate the predicted alpha diversity and the residuals for the excluded 20% plots. In this way we obtained a validation data set of 222 predicted values and their residuals. We examined the normality of residuals with Q–Q plots and histograms. Additionally we controlled for possible anomalies in the models by plotting the residuals against the predicted values, and against each one of the independent variables (Afifi and Clark, 1984). Then, we calculated the linear regression between the predicted and observed alpha diversity, and calculated the confidence intervals (95%) for the slope and intercept to test if these parameters differ from 1 and 0 respectively. Finally, to obtain a unique predictive model, we re-estimated the coefficients of the variables by performing a regression using all the 222 samples.

2.3.3. Beta diversity

Different indices have been proposed to estimate beta diversity, i.e. the species composition variability among sites (Vellend, 2001; Melo et al., 2009). Whittaker (1972) proposed to calculate beta diversity as the inverse of the average proportion in which each species is present in a pool of sites (sampling plots) representative of a landscape. When multiplied by the average alpha diversity, this estimator of beta diversity gives the total number of species in the landscape (gamma diversity). The attractiveness of Whittaker's calculations is that the three diversity indices are connected by a simple mathematical operation, but the problem is that this index is sensitive to the number of plots (Vellend, 2001). It can vary between 1, when all the plots have exactly the same species composition and N (the total number of plots), if all the plots have a completely different composition. An alternative approach would be to calculate all possible pair-wise dissimilarity indices between plots, and then average (Vellend, 2001). We decided to use this last approach, with the beta diversity index proposed by Whittaker to calculate pair-wise dissimilarities. This index, when applied to a pair of samples, is equivalent to the Soerensen dissimilarity index +1 (Vellend, 2001). In this way, the average for any landscape can vary between 1 and 2, independently of the number of sampling plots considered.

To obtain a model to predict pair-wise beta diversity, we calculated the beta diversity index of Whittaker (β_w) for all possible combinations of two plots (i.e. 24,531 pairs). For each pair, we also calculated the absolute differences in the values of the variables listed in Table 1 and the geographical distance between both plots. To normalize the dependent variable (β_w), we applied a modified logit transformation, in the following way:

$$\beta_w(\text{logit}) = \text{Ln}((\beta_w - 1.1)/(1 - (\beta_w - 1.1)))$$

We decided on this transformation because it produced the best distribution of residuals. Then we choose at random the 80% of the pairs (19,647 pairs), with the restriction that all plots should be equally represented in this sub-sample. This precaution was taken to avoid that some plots have more influence than others in the posterior analysis. Using the 80% of the data set, we selected the best predictive model for beta diversity by multiple regression, using a manual backward stepwise procedure. In this case, we expected a beta diversity increase with increasing values of the predictor variables (i.e. absolute differences among plots in physical and physiognomic characteristics, and geographical distance). Thus, we only tested linear, logarithmic (or square root for

variables with zeros) and monotonic quadratic relationships (i.e. using only the quadratic term), but not unimodal relationships. To avoid over-fitting due to the high number of data not completely independent we only selected variables with $P < 0.001$. After selecting the best model, we performed correlations among predictors, to avoid including strongly correlated variables. Additionally, we performed 100 random permutations and compared the distribution of t values in the randomized regressions with the observed t values in the model. In this way we corroborated that the effect of the selected variables on beta diversity differed from chance (Vellend, 2001).

Finally, we calculated the predicted value and residuals for remaining 20% of the pairs. We calculated the regression between predicted and measured beta values, to test if the intercept and slope differed from zero and one respectively. We examined the normality of residuals by Q–Q plots and histograms.

2.3.4. Gamma diversity

To test the relationships of predicted alpha and beta diversity with gamma diversity (defined as the total number of species detected in a landscape), we needed a number of different landscapes as units of analysis. We simulated our landscapes by grouping plots according to geographical proximity. We considered four alternative schemes. First, we randomly discarded two plots and classified the 220 remaining plots in groups of 5, 10 or 20, obtaining in this way three schemes of 44, 22 and 11 simulated landscapes. Additionally, we considered a fourth scheme where each landscape was a management unit (paddock or grazing area), represented by different number of plots (a total of 25 landscapes represented by 4–31 plots, depending on the area). For each landscape of the four schemes we computed gamma diversity.

Based in the predictive models previously obtained, we calculated the predicted alpha diversity for all plots in each landscape, and the predicted beta diversity for all possible pair of plots. Both predicted set of values were then averaged per landscape.

For each scheme, we performed a multiple regression with gamma diversity as dependent variable, and predicted average alpha and beta diversity as independent variables. For the fourth scheme, we also considered the total number of plots (ln transformed) as independent variable, because when gamma diversity is measured simply as the number of species detected in the landscape, it is sensitive to the sampling effort, independently of other factors considered (Gotelli and Colwell, 2001). We also considered all interaction (product) terms. In all cases, we discarded non significant independent variables or terms. All data analyses were carried on with Infostat (2002).

3. Results

We recorded a total of 288 species in the 222 plots, with a plot minimum of five and a maximum of 74 species. The most frequent were *D. hieronymi* (185 plots), *Carex fuscata* d'Urv. (155 plots), *Lachemilla pinnata* (Ruiz and Pav.) Rothm. (147 plots), and *Eryngium agavifolium* Griseb. (146 plots). Accordingly, thin tussock grasses, perennial graminoids and short forbs were the most frequent growth-forms (all present in more than 200 plots), while cacti, trees and ferns were the less frequent growth-forms. In terms of the number of species, we found 132 short forbs, 77 perennial graminoids and 22 ferns, while the remaining growth-forms were far less represented.

3.1. Alpha diversity

In the first run, the five data-sets (80% of the plots each) produced models with slightly different sets of predictor variables.

After our second selection procedure, five variables remained: lawn cover, structural richness, soil depth, local insolation and landscape roughness. The five r^2 values varied from 0.648 to 0.673. When the model was run with all the data ($N = 222$), r^2 was 0.657. According to these models, the highest number of species was found in plots with shallow soils, located at sunny sites in rough landscapes, half covered with lawns (i.e. the sum of short forbs, short perennial graminoids and short annual graminoids was around 50%), and with high structural richness (Fig. 1a–e). The variables rock exposed by erosion, altitude, thick tussock grasses and thin tussock grasses were significant for some of the five data-sets but not for others, and for this reason they were not used as predictors. The r^2 values of the regression between predicted values (calculated for each plot from the model obtained without that plot) and the observed alpha diversity was 0.615. The slope and intercept of the fitting line did not differ from one and zero respectively, validating the five models and thus the final model using all data (Fig. 1f). Residuals were normally distributed.

3.2. Beta diversity

As expected, pair-wise beta diversity increased with the differences between plots in physical and physiognomic characteristics (Table 2). The differences in thick tussock grass cover, lawn cover, and structural richness were the three most important predictor variables. Following were the differences in outcrops, altitude, slope and geographical distance. Finally, the weaker variables in the model were the differences in bare surface (bare soil, lichens and mosses), rock exposed by erosion, soil depth, woody cover and thin tussock grass cover. Local insolation, landscape topographic position and landscape roughness were not selected. The r^2 of the model was 0.45. The relationship between predicted and observed values for the 4884 pairs used for validation had a slope and intercept not different from zero and one respectively, and the r^2 was 0.44. Residuals were normally distributed.

3.3. Gamma diversity

For the four schemes tested, predicted average alpha and beta diversity combined explained a large proportion of variance in observed gamma diversity ($r^2 = 0.77, 0.87, 0.91$ and 0.92 for landscapes represented by 5, 10, 20 and variable number of samples respectively). As expected, for the last scheme the sampling effort (number of plots) was also significant (Fig. 2). Interaction terms were never significant, so they were discarded from the regression models.

4. Discussion

We found a good predictive model for alpha diversity, a reasonable predictive model for pair-wise beta diversity, and a fairly good potential of these models to be combined to predict gamma diversity. To our knowledge this is the first study which developed models to predict the three levels of diversity simultaneously, based in easy to measure field indicators. This provides a powerful monitoring tool for plant diversity, as well trained field biologists are scarce, and they usually do not form part of government agency staff, particularly in developing countries (Danielsen et al., 2008; Holck, 2008).

In our models, variables that predict diversity can be classified as independent or dependent regarding management. Independent variables, such as landscape roughness and slope aspect are physical indicators fixed to each plot (or its surrounding landscape), and by their very nature do not change with management. Management-dependent variables, such as soil depth or lawn cover, are

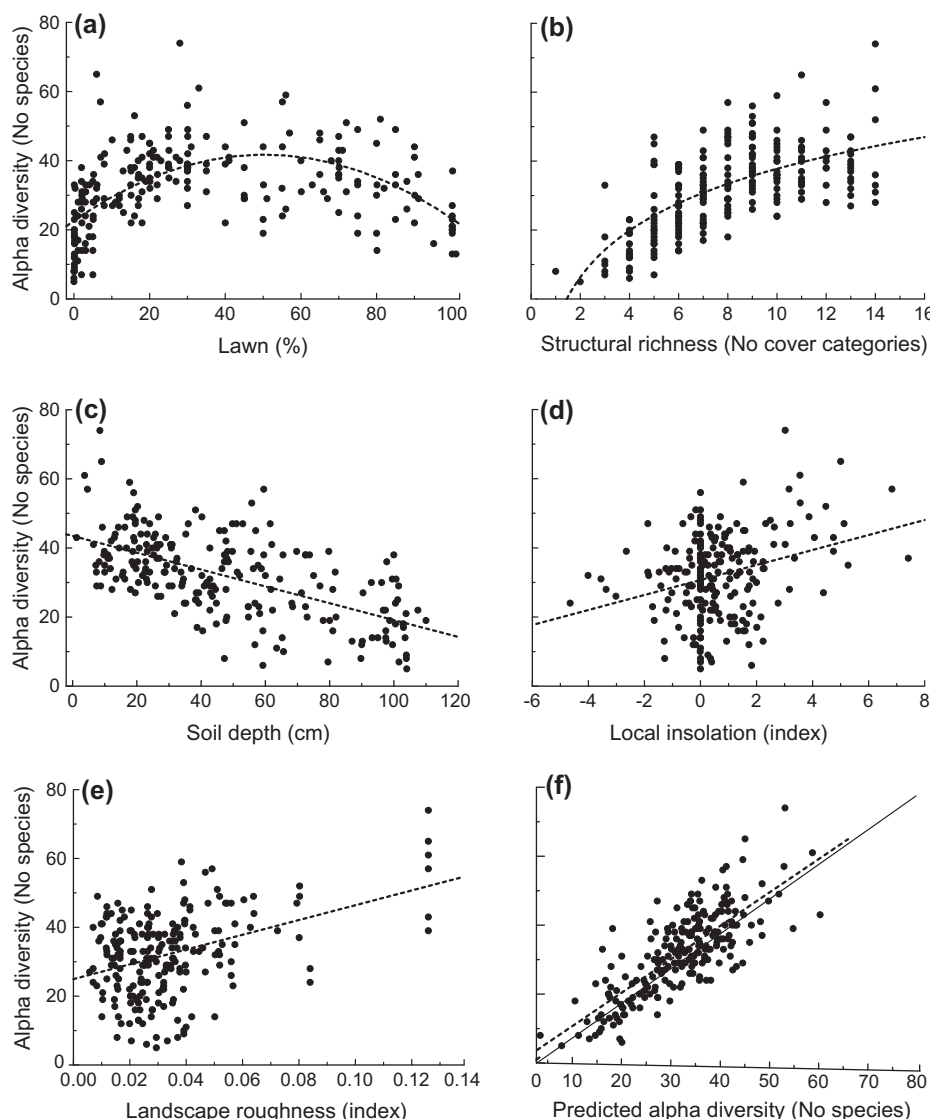


Fig. 1. (a–e) Observed alpha diversity per 16 m² plot against selected predictor variables (circles), and the best fit curve for each case (dashed). (f) Observed alpha diversity against predicted alpha diversity (circles) calculated using a jackknife procedure. Solid line represent the 1:1 relationship and dotted line the best fit line. The final predictor model was: $\text{predicted_alpha_diversity} = 7.1814 + 0.4714 \times \text{Lawn} - 0.0046 \times (\text{Lawn})^2 + 9.2302 \times \text{Ln}(\text{structural richness}) + 111.4958 \times \text{landscape_roughness} - 0.087 \times \text{soil_depth} + 0.9919 \times \text{local_insolation}$.

Table 2
Linear predictive model for beta diversity (logit transformed).

	<i>B</i>	<i>t</i> ^a
Intercept	-1.2646	-43.1
Thick tussock grass cover _(dif) ^{0.5}	7.7×10^{-02}	61.0
Lawn _(dif) ^{0.5}	6.1×10^{-05}	44.0
Structural richness _(dif)	6.0×10^{-02}	33.8
Outcrops _(dif)	8.8×10^{-03}	21.1
Altitude _(dif)	8.3×10^{-04}	20.6
Slope _(dif) ^{0.5}	6.1×10^{-02}	19.9
Ln (geographic distance)	5.7×10^{-02}	17.5
Soil depth _(dif) ^{0.5}	2.5×10^{-02}	14.6
Rock exposed by erosion _(dif)	2.3×10^{-03}	10.8
Bare surface _(dif)	3.3×10^{-03}	7.9
Woody _(dif)	2.6×10^{-03}	7.2
Thin tussock grass cover _(dif)	9.8×10^{-04}	6.8

^a In all cases *t* values were statistically significant ($P < 0.001$), and higher than *t* values obtained from 100 random permutations.

physical or biological indicators sensitive to changes in fire and grazing regimes (Renison et al., 2002; Cingolani et al., 2003, 2008b). These are the most useful variables for our purposes, because they allow tracking off the changes in diversity owed to human decisions (Landsberg and Crowley, 2004). Models to predict or explain the number of plant species have generally been developed using coarse resolution landscape indicators taken from GIS and/or satellite images (e.g. Iverson and Prasad, 1998; Lobo et al., 2001; Moser et al., 2005; Ranjeet et al., 2008). Less common are models developed upon the use of field data (e.g. Wilson et al., 2003; Chiarucci and Bonini, 2005) or a combination of GIS and field data (e.g. Dumortier et al., 2002). Our models for alpha and beta diversity (and hence gamma) are based mainly in fine-resolution field indicators, allowing an early detection of community and landscape trends. With our approach, it is possible to monitor changes in diversity at any scale according to particular needs. For example, we can track the changes in alpha, beta and gamma diversity in the National Park as compared with the Provincial Reserve, or alternatively, we can compare those changes among

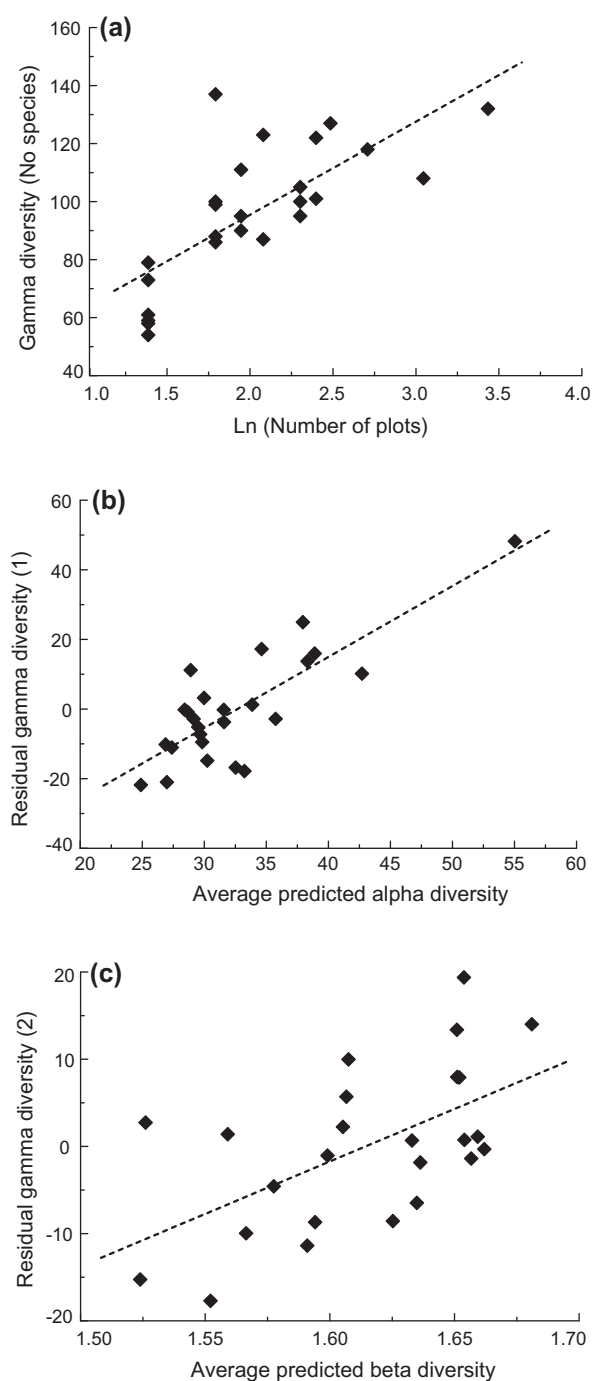


Fig. 2. (a) Observed gamma diversity (number of species detected in a landscape) against sampling effort for simulated landscapes (diamonds) represented by variable number of plots. (b) Residual gamma diversity (i.e. not explained by the number of plots) against predicted average alpha diversity for each landscape. (c) Residual gamma diversity (not explained by the number of plots nor by average alpha diversity) against predicted beta diversity. Dashed lines represent the best fit curves. The regression model including all variables was: $\text{gamma_diversity} = 335.82 + 30.119 \times \text{Ln}(\text{number_of_plots}) + 2.634 \times \text{predicted_average_alpha_diversity} + 176.606 \times \text{predicted_average_beta_diversity}$.

different paddocks within the Park. This is possible because our beta diversity model is based on pairs of plots, and plots can be flexibly combined to represent different landscapes. Additionally, our results for gamma diversity indicate that the predictions can be standardized by sampling effort, which is a necessary step for comparison purposes (Gotelli and Colwell, 2001; Chiarucci and Bonini, 2005; Chiarucci et al., 2008).

Our model explained about 66% of plant alpha diversity, which is a similar value to that obtained by Chiarucci and Bonini (2005), for predicting alpha diversity in Tuscan forests. In line with our results, they found that a combination of management dependent (e.g. stem density) and independent (altitude) variables were optimal to predict plant richness at plot level. In our case, structural richness, soil depth and lawn cover were important predictors. These three variables are highly sensitive to management and are also influenced by topography and natural rockiness. Richer sites were those with shallow soils, half covered with lawn vegetation and structurally heterogeneous. A high structural heterogeneity is linked with high microsite heterogeneity, a factor which generally favors plant diversity at small scales (Lundholm, 2009). In our study area, conditions supporting the highest number of species are found in naturally rocky sites or in sites partially degraded by livestock (Cingolani et al., 2003, 2008b). Conversely, the poorest sites are those on deep soils, with low structural heterogeneity and scarce lawn vegetation. These conditions are common in non-degraded sites under light grazing or livestock exclusion, where tussock grasses strongly dominate the community (Cantero et al., 1999; Cingolani et al., 2003). Competitive dominance of tall grasses is a common response to grazing exclusion in many productive grasslands (McNaughton, 1985; Osem et al., 2002). An exception in our study area are sites close to woodlands, where the proximity of seed rain from *P. australis* trees allows the occurrence of this species (Torres et al., 2008), increasing structural richness. This is associated with an increase in alpha diversity, even at sites on deep and well preserved soils under livestock exclusion. Landscape roughness, a physical factor independent from management also helps explain richness. In our study area, landscape roughness reflects the heterogeneity of the matrix surrounding the stand (Cingolani et al., 2008b) and probably the size of the species pool, which in turn can influence on plot richness (Cantero et al., 1999; Dauber et al., 2003). Finally, local insolation weakly influenced alpha diversity, probably because of the more xeric and warmer conditions created at sunny slopes (Cingolani et al., 2003).

Pair-wise beta diversity was moderately well predicted by physical and physiological differences between the plots. Differences in environmental variables were found to be good predictors of beta diversity for birds and mammals (Melo et al., 2009), and for cacti (Mourelle and Ezcurra, 1997). In the same line, numerous studies found that heterogeneous landscapes (both in terms of physiognomy and physical variables) have higher richness of plants and other taxa (Lobo et al., 2001; Dumortier et al., 2002). The most accepted explanation of species turnover along environmental gradients is the different physiological and ecological tolerance of species to external conditions, including those created by other species (Faith and Walker, 1996). Besides physical and physiological dissimilarity, we found that geographical distance *per se* contributes to predict beta diversity between plots. This is an expected result because species have limited dispersion capacity, generating spatial autocorrelation in their occurrences (Lawrence-Lodge et al., 2007). When beta diversity is estimated for a whole landscape by averaging the predicted values of all component pairs of plots, larger landscapes will have higher predicted beta diversity averages (other factors being equal) as a result of higher number of pairs separated by larger distances. Since predicted beta diversity is used to estimate gamma diversity, the variable "geographical distance" incorporates into our estimations the effect of the landscape area. This is very important because the well known and widely documented species–area relationship should not be ignored when comparing diversity or diversity trajectories among landscapes of different sizes (Adler et al., 2005; Chiarucci et al., 2008; Harte et al., 2009).

Some 92% of gamma diversity variability among landscapes was explained by the average predicted beta and average predicted

alpha diversity combined with sampling effort (number of plots in the landscape). This value is higher than values obtained for models focused directly on gamma diversity, generally based on the use of GIS and satellite variables only, which characteristically explain 60–85% of variance (e.g. Mourelle and Ezcurra, 1996; Lobo et al., 2001; Dumortier et al., 2002). However, we considered this model as preliminary, because it is additive and does not reflect the interactive nature of the relationships between alpha diversity, beta diversity and the number of plots. Because the interaction terms were not significant, we considered that the biases were very small, but more exploration of the data is needed to obtain a more realistic predictive model for gamma diversity.

A first step to tackle the global biodiversity crisis is to develop monitoring programs to track changes (Danielsen et al., 2008; Henry et al., 2008). To be realistic, these programs should be able to be carried out by non expert people, and with low budgets (Pereira and Cooper, 2006; Henry et al., 2008). Our study reaches those aims for the Córdoba mountains. Future research would be needed to test this and alternative approaches in other ecosystems, land uses or threats.

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