

Research article

Consequences of landscape heterogeneity on grassland diversity and productivity in the Espinal agroforestry system of central Chile

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Abstract

The current land use system in the anthropogenic savannas (*Espinales*) of the Mediterranean climate region of Chile, has resulted in considerable heterogeneity at the landscape level which is associated with different covers of the legume tree, *Acacia caven*. The effects of landscape heterogeneity on the diversity and productivity of herbaceous plant communities were studied in 29 plots of 1000 m², with a wide range of woody cover. A detrended correspondence analysis of the species × plots matrix explained 73% of the total variation and revealed the existence of two trends of variation in floristic composition: one associated with physiographic position (hillsides and flatlands) and the other related to the number of years since the last cutting, or coppicing, of *A. caven*. Despite the great majority of the original herbaceous species having disappeared as a result of the prevailing land use system, some native species have been able to survive especially on hillside areas with low grazing intensity. Woody cover was a good indicator of spatial heterogeneity and land use history. It was also correlated with stocking rate, above-ground biomass of herbaceous vegetation, and soil fertility (organic matter, nitrogen and phosphorus concentration), both on hillsides and flatlands. The relationship between woody cover and herbaceous plant species richness was significant and unimodal in flat land areas, and linear, and marginally significant, on hillsides. The consequences of land use changes on the conservation of the ecological and productive values of grasslands are analyzed.

Introduction

The Espinales represent the most widespread agroforestry system of the unirrigated portions of the Mediterranean climate region of central Chile. They cover about 2 million ha (ca. 30°–36° S) and support approximately 350,000 rural inhabitants. This agroforestry system was created by the

progressive clearing, transformation and fragmentation of indigenous sclerophyllous vegetation (since the 16th century), to permit livestock grazing and annual cereal cropping, in a typical process of neo-Europeanization. This has been followed or accompanied by the gradual invasion of *Acacia caven* (Mol.) Hook et Am. (Gulmon 1977; Armesto and Pickett 1985; Ovalle et al.

1990). The resulting anthropogenic formation presents a complex and heterogeneous, savanna-like structure, with herbaceous and woody strata, the latter consisting mainly of *Acacia caven* (Armesto and Pickett 1985), a tree originating from the Chaco region on the eastern side of the Andean cordillera (Aronson 1992). The original sclerophyllous vegetation (*Maitenus boaria* Mol., *Quillaja saponaria* Mol., *Shynus polygamus* (Cav.) Cabr., *Peumus boldus* Mol., *Cryptocaria alba* (Mol.) Looser, etc.) is still present but in small patches dispersed throughout the area. They have great importance for conservation purposes as the only remnants of the native plant community.

The land use system in the Espinal is based on two basic models, continuous grazing and pasture rotated with annual crops (Ovalle et al. 1990; Ovalle and Del Pozo 1994). The former system is used mainly in flatlands where sheep and cattle graze permanently the herbaceous stratum. In these areas, most of the *A. caven* trees of a particular paddock are cut for charcoal or firewood every 40–60 years. The crop-pasture rotation is mainly used on well-drained hillsides (flatlands are not suitable because of the frequent and prolonged water logging in winter); after the crop phase, a spontaneous grassland emerges. Before ploughing, the above-ground biomass of *A. caven* is cut but it resprouts from tree bases the following year. Depending on the size of the farm, soil quality, and cereal market conditions, the intercropping period varies from 3 to 40 years.

Ecological and socio-economic values of the Espinales are high, as described in Ovalle et al. (1990, 1999) and Arroyo et al. (1999). Plant communities in the Espinales present a high diversity of species and ecotypes (Gulmon 1977; Solbrig et al. 1977; Ovalle and Avendaño 1987; Del Pozo et al. 2002) of both native species and those introduced intentionally or accidentally from Eurasia (Sax 2002). Furthermore, it supports most of the Chilean Mediterranean livestock as well as an important area of dryland cereals. The traditional land use systems which vary from continuous grazing of grassland in flatlands to itinerant rotation with cereal crops in hillsides (Ovalle et al. 1990; Ovalle et al. 1996a), is carried out in small paddocks (2 to 20 ha) leading to a physiognomically heterogeneous landscape formed by patches with different levels of *A. caven* cover. On hillsides where the pasture-crop rotation is intense, the Espinales are

more degraded and present lower cover of *A. caven*, greater water erosion and soil nutrient depletion. By contrast, in flatlands the continuous grazing (and the lack of cropping) allows the development of a higher cover of *A. caven* and better soil conservation (Ovalle et al. 1996a). In both physiographic positions, *A. caven* trees are periodically cut but the disturbed areas recover their woody cover with time.

It is well known that landscape heterogeneity in agroforestry systems is important to explain changes in the value of ecological (species richness, diversity) and productive (turnover, biomass, primary production, etc.) variables of plant communities (Pickett and White 1985; Turner 1987; Huston 1994; Forman 1995; Rosenzweig 1995; Burel and Baudry 2001). The relationships among landscape heterogeneity and ecological and productive parameters of the herbaceous communities have not been quantified in the Espinales, despite their importance for the ecological and agronomic rehabilitation of this agroforestry system (Aronson et al. 1993a,b).

In this article, the relationships between woody cover and ecological and agronomic variables of herbaceous communities in the Chilean Espinales are analyzed for both hillsides and flatlands. Our hypothesis is that landscape heterogeneity could explain the spatial distribution of the above-mentioned variables and that different responses are to be expected on hillsides and flatlands. The consequences that land use change could have on the conservation of ecological and productive values are also analyzed.

Materials and methods

Study area

The study was conducted in the subhumid portion of the Mediterranean climate region of Chile. The area was located near the Experimental Center of Cauquenes-INIA (35°58' S, 72°17' W; 140 m a.s.l.), VII Region, in the eastern part of coastal mountain range. Long term average of the minimum temperatures of the coldest month (July) is 4.8 °C and of the maximum temperatures of the warmest month (January) is 29 °C. Mean annual rainfall is 695 mm. Fire occurs sporadically in the area and is not used as a management tool.

Methods

For the characterization of the herbaceous vegetation of the Espinales, 29 plots of 1000 m² (25×40 m) were set up and distributed along a 23,000 ha transect, which was previously mapped and characterized (Ovalle et al. 1996a), and which covers a wide range of land use (grazing, fallows and cropping). These plots were selected to cover five different Espinal types, or cover classes, occurring on hillsides or plains (0–10%, 11–25%, 26–50%, 51–75% and 76–100%, consisting mainly of *A. caven*). Hillsides corresponded to well-drained areas with slopes greater than 10% and flatlands to plain areas occasionally inundated during winter. The number of plots on each cover class was proportional to its area, and they were distributed at random within each cover class. Climatic conditions were similar in the whole area.

Five groups of variables were evaluated in each plot: (a) physiographic, which included elevation, slope, and assignation to flatland or hillside position according to whether the area suffers flooding or not during winter; (b) species abundance (only herbaceous species, including grasses), evaluated as the relative frequency of contacts every 4 cm in three lines of 4 m in length, within the plot (point quadrat method, Daget and Poissonet 1971); (c) variables related with the structure and function of the community, like cover of the woody strata (trees and shrubs), estimated from cartography of the vegetation on a scale of 1:200, plant richness of herbaceous species (evaluated as number of species in the same three lines of the floristic composition sampling), and above-ground biomass of the herbaceous strata (3–4 exclusion cages of 1 m²); (d) edaphic variables, which included soil N (Kjeldahl method) and organic matter (% using wet combustion with sulphuric acid and determination of the reduced sodium dichromate by colorimeter), P₂O₅ (ppm, Olsen method) and the C:N ratio, determined in the first 20 cm of the mineral horizon (10 soil samples randomly collected in each plot, mixed before the analyses); (e) variables related to land use, such as stocking rate (number of sheep per hectare) and years since last cutting of *A. caven* (determined for all coppice clumps by coring and ring counting of the largest branch of each clump).

Detrended correspondence analysis (DCA) was performed on floristic composition data, using the

similitude index of Bray–Curtis. This analysis was performed taking into account only the species present in more than 3 plots. Regression (linear or polynomic) analyses were used to describe changes in plant richness, above-ground biomass and edaphic variables, using woody cover and years since last tree cutting as the dependent variables. The analyses were carried out using (SAS 2000) and PATN (Belbin 1987) statistical packages.

Results

Woody cover showed a significant ($r = 0.79$; $p < 0.0001$) relationship with years since the last cutting of *A. caven* (Figure 1). The relationships were positive in both hillside and flatland plots but with a higher slope in the latter.

In the 29 plots studied, 79 plant species were identified but only 40 species appeared in more than three plots. The two first axes of the ordination analysis carried out with these 40 species explained 73% of the total variation. Axis 1 represented a gradient between the two physiographic positions segregating plots of flatlands (extreme left) from those of hillsides (extreme right) (Figure 2). This axis was significantly related to topographic position and altitude (Table 1), variables not included in the ordination analysis. The species

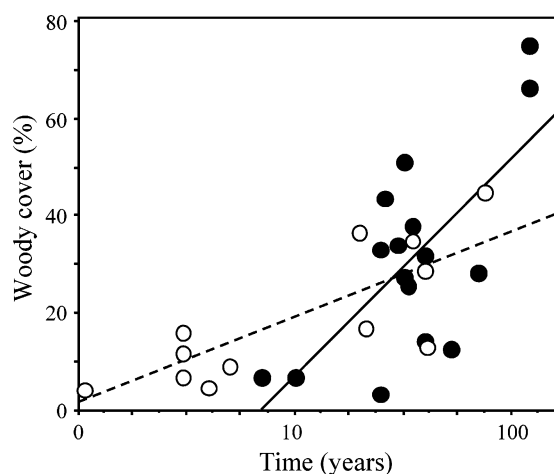


Figure 1. Relationship between years after *A. caven* cutting (log transformed) and woody cover for hillsides (○) dashed line, $r = 0.806$, $p = 0.0009$, and flatlands (●), continuous line, $r = 0.736$, $p = 0.0011$.

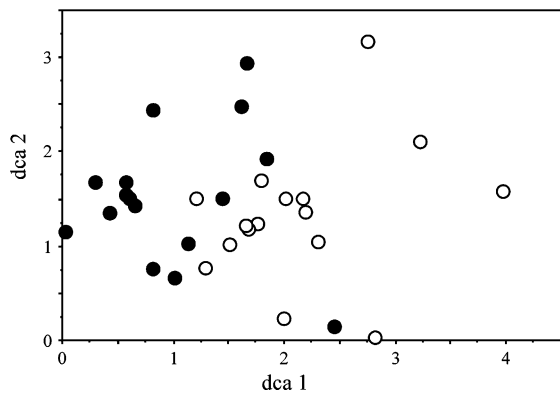


Figure 2. Position of the 29 plots in the first two axes of the detrended correspondence analysis for the relative abundance of herbaceous species for hillsides (○) and flatlands (●). Axes 1 and 2 explained 41 and 32% of the variance, respectively (eigenvalue = 0.53963 and 0.38181; axis length = 3.970 and 3.177). The relationship between these two axes and other descriptive variables of the plots are shown in Table 1.

Table 1. Pearson correlation values between the scores of the detrended correspondence analysis axes (see Figure 2) and descriptive variables of the plots.

	Axis 1	Axis 2
<i>Physiographic variables</i>		
Altitude (m.a.s.l.)	0.54***	0.02
Slope (%)	0.47***	-0.12
Topographic position ^a	22.10***	0.62
<i>Structural and functional variables</i>		
Woody cover (%)	-0.124	0.75***
Above-ground biomass (g m ⁻²)	-0.07	0.68***
Herbaceous species richness	-0.069	0.345*
<i>Edaphic variables</i>		
Organic matter (%)	-0.23	0.47**
N content (%)	-0.19	0.55***
P content (ppm P ₂ O ₅)	0.01	0.56***
C:N	0.23	-0.49**
<i>Land use variable</i>		
Stocking rate (sheep/ha)	-0.44**	0.49**
Years after last <i>A. caven</i> cutting	-0.15	0.704***

* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

^aF value of a one way ANOVA.

that characterized the extreme left of the axis were *Trisetum spicatum* (L.) K. Richt., *Hordeum berteroanum* E. Desv. ex Gay, *Plantago firma* Kunze ex Walp., *Leontodon leysleri* (Wallr) Beck, *Deschampsia berteroana* Fr. Meigen and *Parentucellia latifolia* Caruel. Characteristic species of the extreme right were *Bromus mollis* L., *Stipa laevisissima*, *Erodium botrys* Bertol., *Dichondra*

repens Forst., *Plantago hispidula* Ruiz and Pav. and *Trisetobromus hirtus* (Trin.) Nevski. Axis 2 was correlated with structural and functional vegetation traits (woody cover and above-ground biomass), as well as with edaphic variables (organic matter, N and P concentrations, and C:N ratio) and land use variables (stocking rate and years since last cutting of *A. caven*) (Table 1). All the species correlated with this axis are non-native, originally from the Mediterranean basin and adjacent parts of SW Asia. *Medicago polymorpha* L., *Lolium multiflorum* Lam. and *Carduus pycnocephalus* L. characterized the upper extreme of the axis whereas *Avena barbata* Link, *Taeniatherum caput-medusae* (L.) Nevski and *Aira caryophyllaea* L. characterized the lower extreme of the axis.

Significant differences ($p < 0.05$) between hillsides and flatlands were found in stocking rate, organic matter and N concentration, and the C:N ratio of the soil (Table 2). Woody cover tended to be marginally greater in flatlands ($p = 0.057$). No differences were found in plant species richness and above-ground herbaceous biomass.

Stocking rate showed positive correlations with woody cover, both for the entire data set (hillside and flat land plots together, $r = 0.71$; $p < 0.0001$) and for hillsides and flatlands plots separately (Figure 3). The relationship between herbaceous richness and woody cover was significant ($r = 0.64$; $p < 0.0335$) and unimodal in flatlands, and linear and marginally significant ($r = 0.54$; $p = 0.0574$) on hillsides (Figure 4a). The cumulative herbaceous richness was calculated sorting the plots in three ways: increasing values of woody cover, decreasing values of woody cover and at random (Figure 4b,c). The cumulative richness increased more sharply in both hillsides and flatlands when decreasing values of woody cover were considered.

Above-ground biomass of the herbaceous vegetation increased significantly with woody cover (Figure 5a; $r = 0.89$ and $r = 0.82$ for hillsides and flatlands, respectively; $p < 0.001$ for both cases). Soil parameters, such organic matter, nitrogen, and phosphorus concentration, increased significantly with increasing woody cover, in both hillsides and flatlands (Figures 5b-d; for all cases $r > 0.76$; $p < 0.001$), but the C:N ratio decreased (Figure 5e; $r = -0.85$, $p = 0.002$ and $r = -0.56$, $p = 0.023$, for hillsides and flatlands, respectively).

Table 2. Mean values (and standard deviation) for structural, edaphic and ecological variables in hillsides ($n = 13$) and flatlands ($n = 16$) in the Chilean Espinales. F values and probability (p) are also shown.

	Hillside espinales	Flat land espinales	F	p
Woody cover (%)	17.9 (13.9)	31.3 (20.6)	3.96	0.0567
Stocking rate (sheep ha ⁻¹)	1.19 (0.66)	2.56 (0.87)	21.76	0.0001
Above-ground herbaceous biomass (kg ha ⁻¹ year ⁻¹)	704.5 (656.5)	1243.2 (910.0)	3.19	0.0852
Herbaceous species richness	15.0 (4.3)	14.5 (2.9)	0.14	0.7119
Soil organic matter (%)	1.4 (0.60)	2.8 (0.94)	19.93	0.0001
Soil nitrogen (%)	0.16 (0.05)	0.24 (0.06)	14.55	0.0007
Soil phosphorus (ppm P ₂ O ₅)	2.7 (0.68)	3.3 (1.27)	2.36	0.1363
C:N ratio	6.82 (0.67)	6.11 (0.60)	9.13	0.0054

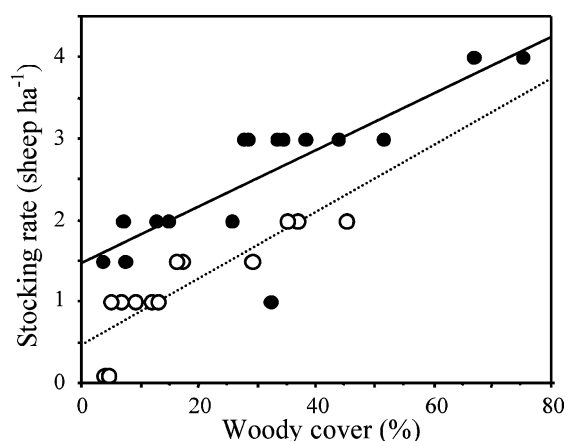


Figure 3. Relationship between woody cover and stocking rate for hillsides (○, dashed line; $r = 0.82$, $p < 0.0001$) and flatlands (●, continues line; $r = 0.86$, $p = 0.0002$).

Discussion

Land use change from the original vegetation and its transformation to grassland or cropping systems have had great impacts on the ecosystem, resulting in almost total eradication of the woody sclerophyllous vegetation (e.g., *Quillaja saponaria*, *Maitenus boaria*, *Peumus boldus*, *Cryptocaria alba*, etc.), and the secondary predominance of *A. cavem* in the new agroforestry system matrix (Armesto and Pickett 1985; Ovalle et al. 1990). Furthermore, the transformation of the Espinales into a cropping system has led to a marked decline in soil-borne organic matter and macronutrients (Figure 5). In fact, on hillsides under intensive cereal-pasture rotation, and with very low cover of *A. cavem*, soil organic matter levels were half those found in the flatlands (high woody cover; permanent grazing).

The contemporary land use system of the Espinales has resulted in large landscape heterogeneity, which is highly related to cover of *A. cavem*. The structure in mosaic of the landscape is a common feature of many Mediterranean agroforestry systems, like the Spanish “dehesas”, and represents an adjustment of the traditional management practices to environmental possibilities of the territory (de Miguel 1999). In the case of the Espinales the spatial variation of woody cover is a good descriptor of landscape heterogeneity and the cover value can be used as an indicator of recent land use history of a sector, e.g., years since the last cropping and cutting of the *A. cavem*. Other common land use parameters, like stocking rate, provide more limited information. The stocking rate depends on farmers’ immediate necessities and on how animals use the space and resources within a paddock (Gómez-Sal et al. 1992; de Miguel et al. 1997). It is therefore highly variable in time and in space and less reliable as an indicator.

In the Espinales, woody cover can be severely reduced as a consequence of land use changes, like ploughing for cereal cropping in hillsides, or exploitation of *A. cavem* for charcoal or firewood in flatlands under permanent grazing. However, recuperation of the cover of *A. cavem* takes place over several years after the perturbation, at a rate of ca. 5% every 10 years (Figure 1). The positive correlation between woody cover and stocking rate (Figure 3) is probably a consequence of the direct relationship that exists between the above-ground herbaceous biomass and woody cover (Figure 5a).

The heterogeneity associated to woody cover has important consequences on botanical composition (floristic variation) and for ecological (species

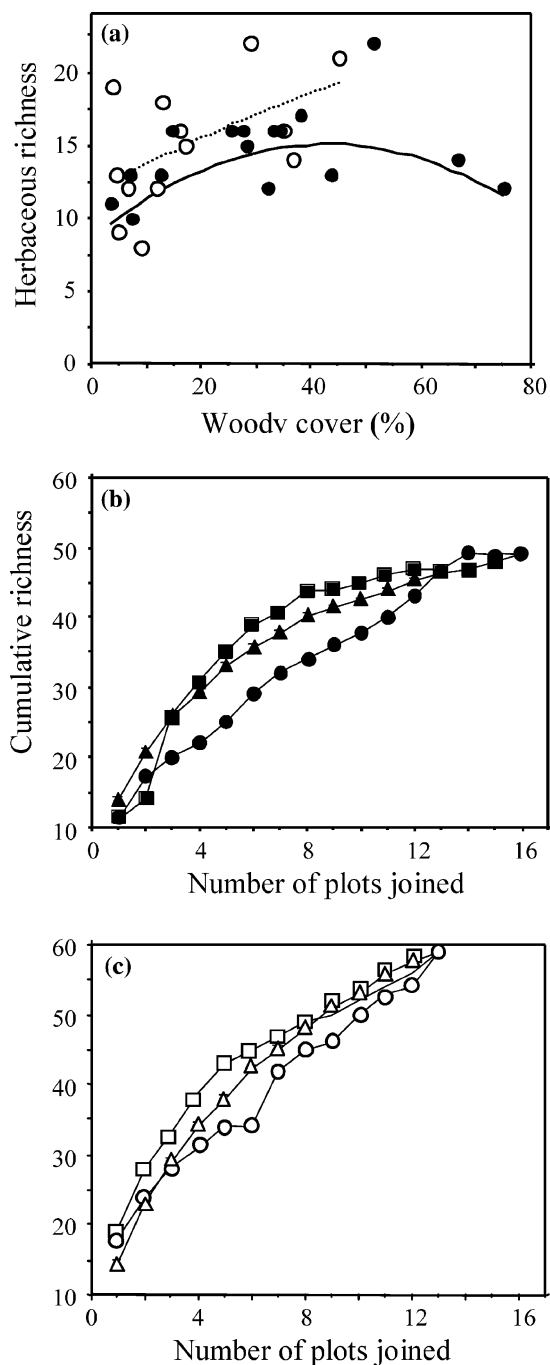


Figure 4. Relationship between woody cover and herbaceous richness (a), and cumulative herbaceous richness for hillsides (b) and flatlands (c). In (a) closed circles and continuous line are for flatlands, and open circles and dashed line for hillsides. In (b) and (c) plots were sorted according to increasing woody cover (circles), decreasing woody cover (squares) and by adding plots randomly (triangles, mean and SD values after repeating this process 20 times). Standard errors are smaller than the size of the symbols.

richness) and agronomic (biomass and soil fertility) values of grasslands. The results of the ordination analysis show the existence of two floristic trends of variation, one associated with environmental variability (Axis 1) and the other related to land use history (Axis 2; Figure 2). The floristic differentiation between hillsides and flatlands is probably a consequence of differences in water regime between these two physiographic positions, with more favourable water regime and greater organic matter and nitrogen content occurring in soils of flatlands than on hillsides (Table 2). It is noteworthy that many of the species of hillsides (left extreme of axis 1) are natives, despite the fact that the history of land use has drastically diminished the richness of native herbaceous species (Aronson et al. 1998; Holmgren et al. 2000). Accordingly, some native species have been able to colonize areas on hillsides, especially the less grazed ones, even though such areas have been frequently ploughed in the past.

The floristic differentiation observed along Axis 2 had a positive correlation with land use variables, such as woody cover, stocking rate and years since last tree cutting (Table 1). All the species correlated with Axis 2 came from the Mediterranean basin where they are associated with farming (Rivas-Martínez 1977). In areas of low woody cover and therefore with recent land perturbation (ploughing or tree cutting), the characteristic species are *Avena barbata*, *Taeniatrum caput-medusae* and *Aira caryophyllea*. These species are common in uncultivated or old fields (Rivas-Martínez and Izco 1977) and have had many centuries, or millennia, to adapt to the perturbations produced by agrarian practices in the Mediterranean basin (Noy-Meir and Seligman 1979; Noy-Meir et al. 1989). These practices are similar or identical to those farming systems introduced in Chile by the Spaniards during the colonial period, and therefore the abundance of these species in recently disturbed plots is not surprising. In areas of high woody cover, the characteristic species are *Medicago polymorpha*, *Lolium multiflorum* and *Carduus pycnocephalus*, which are typical in Mediterranean Spain of sites rich in nitrogen and intensive grazing (Rivas-Martínez 1978). They have been favoured by the existence of a high stocking rate in the Espinales, an uncommon condition in Chile before European colonization.

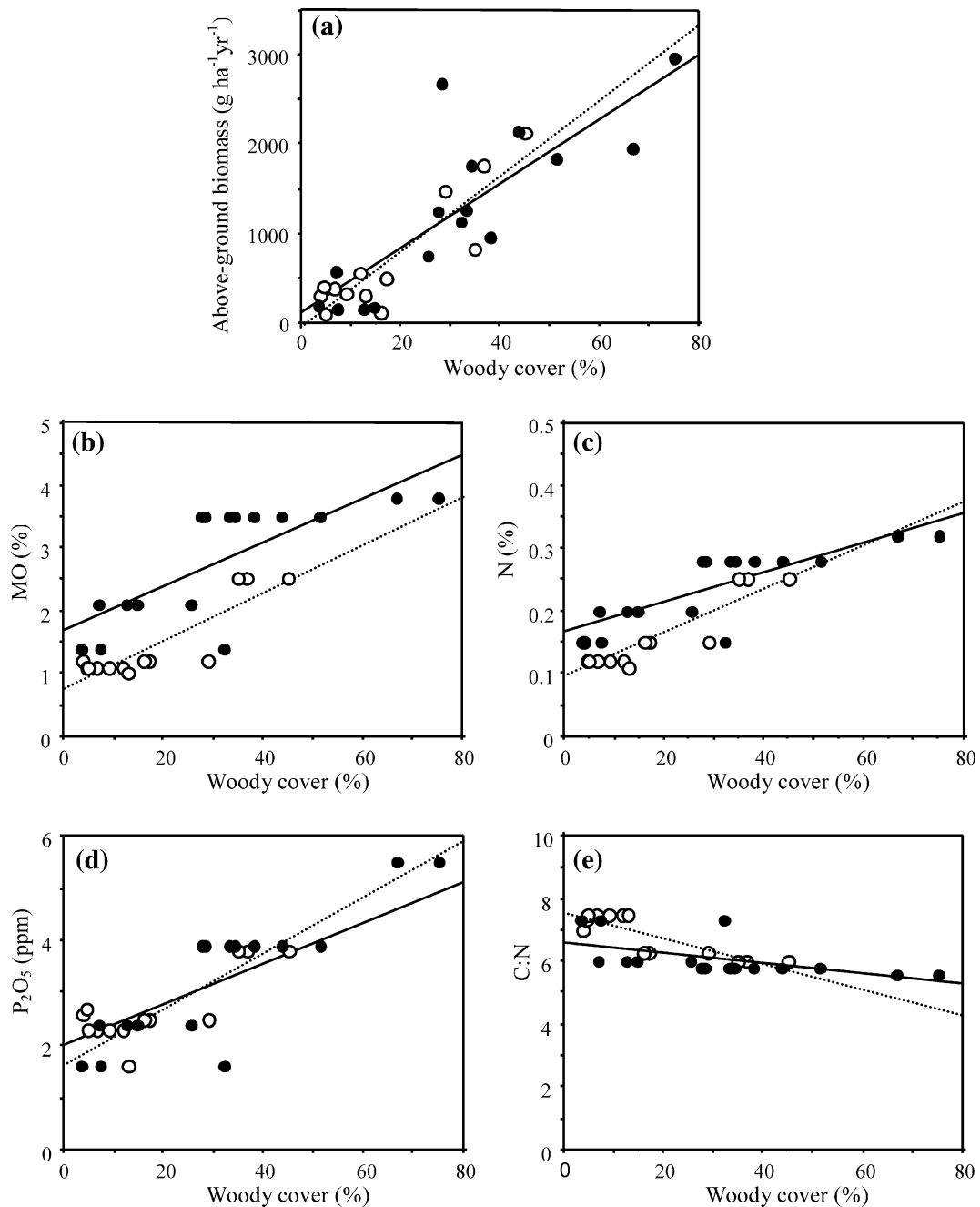


Figure 5. Relationships between woody cover and above-ground biomass (a), the content of organic matter (b), nitrogen (c), phosphorus (d) and C:N ratio (e) in soils (0–20 cm), for hillsides (○, dashed line) and flatlands (●, continuous line). All regression lines were significant ($p < 0.001$).

Despite the fact that clear differences between hillside and flatland were detected in floristic composition (Figure 2) and in soil fertility, no significant ($p > 0.05$) differences were observed in biomass and numbers of herbaceous species

(Table 2). In similar studies conducted on lower and upper slope zones in semiarid Mediterranean grasslands of Spain, values in biomass and species richness differed according to the stage of ecological succession (Casado et al. 1985). In our study

area, the various land use systems in each topographic position could mask these differences. Woody cover seems to be determinant to explain the biomass and richness of the herbaceous vegetation.

The relationship between woody cover and plant species richness is clearly unimodal in flatlands but not on hillsides (Figure 4a), where it tends to be monotonic, probably due to a more limited range of woody cover values. On hillsides, where woody cover was lower than 50%, the positive linear relationship observed can correspond to the ascending branch of a common humped curve for both physiographic positions (Casado et al. 2004). This unimodal pattern is similar to that predicted by the theory of intermediate perturbation (Connell 1978). The maximum richness in a plot is obtained at intermediate values of woody cover (around 40%) and therefore at an intermediate number of years after tree cutting. This result predicts that herbaceous plant richness depends on the frequency of perturbation in the Espinales. When the frequency of perturbation is high the woody cover is maintained in values lower than 40%, whereas under very low perturbation frequency woody cover increases to greater values diminishing the specific richness of the herbaceous vegetation. The variation in richness with woody cover does not necessarily represent a direct causal-effect relationship. Rather, it can be the result of several different factors acting simultaneously (Pauses and Austin 2001), such as productivity (Figure 5a) or nutrient gradients (Figure 5b,c,d), or light attenuation in the woody canopy (Grace 1999). However, independently of the governing factor, woody cover can be used as an indicator of herbaceous species richness.

The pattern followed by the accumulated richness with woody cover (Figures 4b,c) reveals the importance of landscape heterogeneity on maintaining a high beta diversity in the Espinales. In both hillsides and flatlands, patches with higher woody cover incorporate more species to the regional richness than patches with lower woody cover. For instance, in flatlands, selecting the 50% of the plots with the highest woody cover, almost 90% of the total richness is obtained, whereas selecting the 50% of the plots with lowest woody cover, incorporates only the 70% to the total species richness (Figure 4b). These results seem to indicate a greater floristic uniformity within pat-

ches of lower woody cover, which agree with the successional divergence found in Mediterranean grasslands in central Spain (Pineda et al. 1981).

Farmers prefer sites with high cover of *A. caven* because they are more productive (Figure 5a) and can sustain greater stocking rates (Figure 3). This preference is consistent with the greater content of organic matter, nitrogen and phosphorus in soils in sites of high woody cover (Figures 5c,d,e). The effects of *A. caven* cover on soil fertility are related to the nutrient recycling through animal grazing, the contribution of leaves and stems that fall from trees (Ovalle and Avendaño 1987), and the biological nitrogen fixation capacity of *A. caven* (Ovalle et al. 1996b; Aronson et al. 2002).

In conclusion, landscape heterogeneity in the Espinales, as generated by the physiographic position (hillsides and flatlands) and the range of woody cover, results in important floristic differentiation of the herbaceous vegetation. Woody cover is related to the frequency with which the *A. caven* is cut and has an important practical value for the planning and management of grassland resources, since it can be easily recognized in the field. Also, it has important consequences on various ecological or productive variables of the herbaceous vegetation. The maximum values of herbaceous species richness and biomass are attained at medium and high values of woody cover, respectively. These patterns of variation allow to predict the consequences of various scenarios of land use. One extreme would be the intensification of the cereal production, which would imply frequent tree cutting and the loss of both soil fertility and herbaceous species richness. The other extreme would be permanent grazing that would imply an increase in woody cover, and of soil fertility and grassland biomass, but a decrease in species richness. An intermediate situation would be intermediate woody cover (about 50%), which allows the existence of high species diversity and a high biomass production of grassland. This situation can be achieved with a frequency of cutting of about 60 years, very close to that traditionally used in the Espinales.

From the ecological and agronomic point of view, the intensification of the cereal-pasture rotation as a management practice is the worst scenario for the Espinales. On the contrary, the restoration of the degraded Espinales in order to increase woody cover up to 50% or more would

increase the naturalistic values and the stocking rate capacity of the region.

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