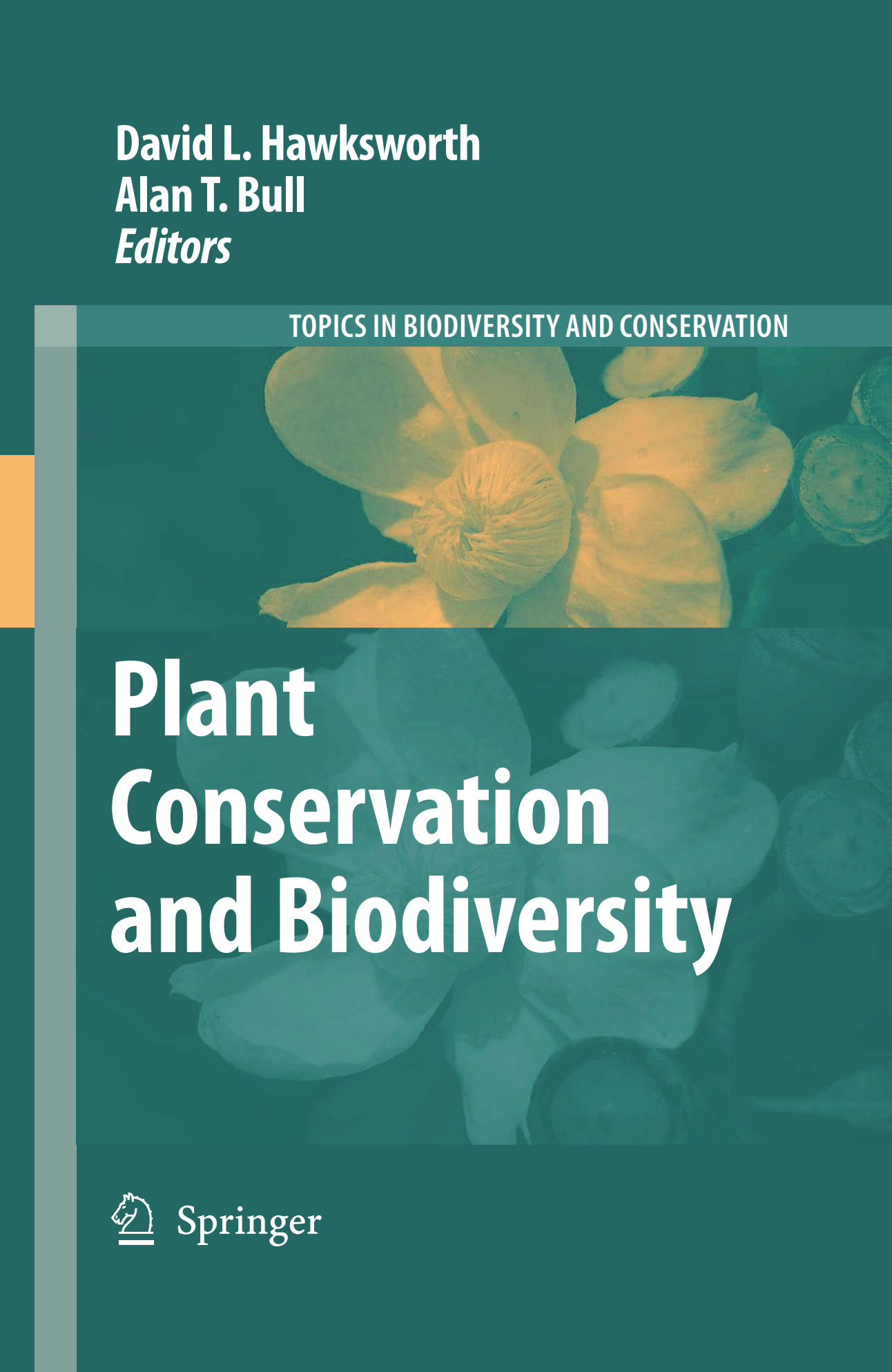


David L. Hawksworth
Alan T. Bull
Editors

TOPICS IN BIODIVERSITY AND CONSERVATION



Plant Conservation and Biodiversity



Springer

Plant Conservation and Biodiversity

TOPICS IN BIODIVERSITY AND CONSERVATION

Volume 6

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Plant Conservation and Biodiversity

Edited by

David L. Hawksworth

and

Alan T. Bull

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Contents

Plant Conservation and Biodiversity

C. M. GHERSA, S. B. PERELMAN, S. E. BURKART and R. J. C. LEÓN / Floristic and structural changes related to opportunistic soil tilling and pasture planting in grassland communities of the Flooding Pampa	1–18
CARLOS E. VALDIVIA and JAVIER A. SIMONETTI / Decreased frugivory and seed germination rate do not reduce seedling recruitment rates of <i>Aristotelia chilensis</i> in a fragmented forest	19–28
G. KAZAKIS, D. GHOSN, I. N. VOGIATZAKIS and V. P. PAPANASTASIS / Vascular plant diversity and climate change in the alpine zone of the Lefka Ori, Crete	29–41
BETTINA HEIDER, MEIKE S. ANDERSSON and RAINER SCHULTZE-KRAFT / RAPD variation among North Vietnamese <i>Flemingia macrophylla</i> (Willd.) Kuntze ex Merr. accessions	43–57
TAMARA TICKTIN, HÖ'ALA FRAIOLA and A. NĀMAKA WHITEHEAD / Non-timber forest product harvesting in alien-dominated forests: effects of frond-harvest and rainfall on the demography of two native Hawaiian ferns	59–77
PATRICIA COLUNGA-GARCÍAMARÍN and DANIEL ZIZUMBO-VILLARREAL / Tequila and other <i>Agave</i> spirits from west-central Mexico: current germplasm diversity, conservation and origin	79–93
ALEJANDRA JUÁREZ, PABLO ORTEGA-BAES, SILVIA SÜHRING, WALTER MARTIN and GUADALUPE GALÍNDEZ / Spatial patterns of dicot diversity in Argentina	95–103
HELLE OVERGAARD LARSEN and CARSTEN SMITH OLSEN / Unsustainable collection and unfair trade? Uncovering and assessing assumptions regarding Central Himalayan medicinal plant conservation	105–123
ADEMIR R. RUSCHEL, RUBENS O. NODARI and BRUNO M. MOER-SCHBACHER / Woody plant species richness in the Turvo State park, a large remnant of deciduous Atlantic forest, Brazil	125–140
MARCO MANZELLI, LUCA PILERI, NADIA LACERENZA, STEFANO BENEDETTELLI and VINCENZO VECCHIO / Genetic diversity assessment in Somali sorghum (<i>Sorghum bicolor</i> (L.) Moench) accessions using microsatellite markers	141–156
HONGMEI LI, T. MITCHELL AIDE, YOUXIN MA, WENJUN LIU and MIN CAO / Demand for rubber is causing the loss of high diversity rain forest in SW China	157–171
WAYNE LAW and JAN SALICK / Comparing conservation priorities for useful plants among botanists and Tibetan doctors	173–185
JOSÉ ALDO A. PEREIRA, ARY T. OLIVEIRA-FILHO and JOSÉ P. LEMOS-FILHO / Environmental heterogeneity and disturbance by humans control much of the tree species diversity of Atlantic montane forest fragments in SE Brazil	187–210
K. J. HALME and R. E. BODMER / Correspondence between scientific and traditional ecological knowledge: rain forest classification by the non-indigenous ribereños in Peruvian Amazonia	211–227

RAÚL CONTRERAS-MEDINA and ISOLDA LUNA-VEGA / Species richness, endemism and conservation of Mexican gymnosperms	229–247
G. M. FREDRIKSSON, L. S. DANIELSEN and J. E. SWENSON / Impacts of El Niño related drought and forest fires on sun bear fruit resources in lowland dipterocarp forest of East Borneo	249–264
YUAN-WEN DUAN and JIAN-QUAN LIU / Pollinator shift and reproductive performance of the Qinghai–Tibetan Plateau endemic and endangered <i>Swertia przewalskii</i> (<i>Gentianaceae</i>)	265–276
MUKUNDA DEV BEHERA and SATYA PRAKASH SINGH KUSHWAHA / An analysis of altitudinal behavior of tree species in Subansiri district, Eastern Himalaya	277–291
X. SCHELDEMAN, L. WILLEMEN, G. COPPENS D'EECKENBRUGGE, E. ROMEIJN-PEETERS, M. T. RESTREPO, J. ROMERO MOTOCHÉ, D. JIMÉNEZ, M. LOBO, C. I. MEDINA, C. REYES, D. RODRÍGUEZ, J. A. OCAMPO, P. VAN DAMME and P. GOETGEBEUR / Distribution, diversity and environmental adaptation of highland papayas (<i>Vasconcellea</i> spp.) in tropical and subtropical America	293–310
ELOY SOLANO and T. PATRICIA FERIA / Ecological niche modeling and geographic distribution of the genus <i>Polianthes</i> L. (<i>Agavaceae</i>) in Mexico: using niche modeling to improve assessments of risk status	311–326
JOHN R. S. TABUTI / The uses, local perceptions and ecological status of 16 woody species of Gadumire Sub-county, Uganda	327–341
M. IRFAN-ULLAH, GIRIRAJ AMARNATH, M. S. R. MURTHY and A. TOWNSEND PETERSON / Mapping the geographic distribution of <i>Aglaiia bourdillonii</i> Gamble (<i>Meliaceae</i>), an endemic and threatened plant, using ecological niche modeling	343–351
MARTIN RICKER, ILIANA RAMÍREZ-KRAUSS, GUILLERMO IBARRA-MANRÍQUEZ, ESTEBAN MARTÍNEZ, CLARA H. RAMOS, GUADALUPE GONZÁLEZ-MEDELLÍN, GABRIELA GÓMEZ-RODRÍGUEZ, JOSÉ LUIS PALACIO-PRIETO and HÉCTOR M. HERNÁNDEZ / Optimizing conservation of forest diversity: a country-wide approach in Mexico	353–383
DAVID MELICK, XUEFEI YANG and JIANCHU XU / Seeing the wood for the trees: how conservation policies can place greater pressure on village forests in southwest China	385–397
MARIEL AGUILAR-STØEN and STEIN R. MOE / Medicinal plant conservation and management: distribution of wild and cultivated species in eight countries	399–407
XIAO LEI JIANG, WEI GUO ZHANG and GANG WANG / Biodiversity effects on biomass production and invasion resistance in annual versus perennial plant communities	409–420

Introduction

Plant conservation and biodiversity

This book brings together a selection of original studies submitted to *Biodiversity and Conservation* addressing aspects of the conservation and biodiversity of plants. Plants are, along with terrestrial vertebrates, the best known organisms on Earth, and so work on them can be a model for that on less known organism groups. Further, plants are crucial to the maintenance of atmospheric composition, nutrient cycling, and other ecosystem processes. In addition they provide habitats and food for myriads of dependent organisms. At the same time, plants are exploited for food and fuel by humans, and forests continue to be felled for the timber trade or to provide more grazing for cattle. As individual plants are not mobile, and often co-exist as parts of complex plant communities, they are also particularly vulnerable to global climate and other ecological changes.

The contributions are drawn mainly from tropical and subtropical countries, especially Central and South America and Asia, and collectively provide a snapshot of the types of issues and concerns in plant conservation in these regions today. The subjects treated range from effects of climate and habitat changes, including effects of alterations in management and major fires, through the exploitation of forests for medicinal plant and other products as well of trees, to genetic variation within endangered or exploited species, and factors affecting seed production and germination.

This series of themed issues aims to provide an indication of current research activities across this wide range of topics, examples of issues of current concern, that will make the book especially valuable for use in conservation biology courses. They can be viewed as a series of case studies that will expose students to primary research being conducted now. As such they will complement the necessarily less-detailed information available in textbooks and review articles.

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Editor-in-Chief, Biodiversity and Conservation

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25 April 2007

Floristic and structural changes related to opportunistic soil tilling and pasture planting in grassland communities of the Flooding Pampa

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Key words: Biodiversity, Ecological impact, Grassland communities, Landscape diversity, Old pastures, Soil tilling

Abstract. The Flooding Pampa natural grassland has an intricate pattern of plant communities, related to small topographic differences that determine important changes in soil characteristics. Despite limitations imposed by soil properties and periodic waterlogging, opportunistic tilling is carried out to plant pastures. There is little information on how pasture planting may affect the structure of the grassland communities. In order to document changes caused by cultural activities on structural and functional characteristics of plant communities in this landscape, we made field surveys in grasslands and very old pastures (grassland communities recovered through secondary succession) using transects located across existing topographic gradients. The patchy structure of this landscape was revealed by the multivariate analysis, by means of which four plant communities could be identified in the natural grassland. Species composition of these communities differed from that of the corresponding old pastures. They lost an important number of exclusive species, but also gained species: some new to the landscape and many already present in other environments. Pasture planting reduced the rate of species replacements along the gradient and produced changes in patchiness, but had no effect on the species–area curve at the landscape scale. Neither did we find differences in total number of species, average number of species/site and proportion of functional types. The new grassland created by opportunistic pasture planting has developed into a structural gradient in which important differences occurred in the lower waterlogged-prone stands, whereas the sites of the other communities experienced less structural changes.

Introduction

The Flooding Pampa grasslands in eastern Argentina cover 90,000 km² of an extremely flat area with poorly drained soils, which have been extensively modified by anthropogenic disturbances (Chaneton et al. 2002). This natural grassland is heterogeneous and characterized by well-defined plant communities that are strongly correlated with the small topographic differences determining dramatic changes in soil characteristics (Soriano 1992; Perelman et al. 2001). Cattle husbandry on unfertilized natural grasslands has been the main activity in this area, which increased species richness in most of the plant

communities by enhancing invasion of exotics, but also reduced the compositional and functional heterogeneity of the vegetation at landscape scale (Chaneton et al. 2002).

Technological improvements and need to increase the economic revenue of the land is continually pushing ranchers to replace this traditional practice of extensive low input grazing of natural grasslands, by intensive grazing of planted pastures and, in some cases, even cropping of annual species (Cahuepé et al. 1982; Oesterheld and León 1987; De León and Cauhepé 1988; Soriano 1992; Gerschman et al. 2003). For this reason, despite the limitations imposed by soil properties and periodic water logging, opportunistic tilling is carried out to plant pastures, which may remain grazed and without replanting for very long periods of time. Although there are no patterns, these periods frequently extend to 10 years or more, and fields with pastures older than 50 years are not difficult to find. The secondary succession developing after pasture planting in the regions better drained soils has been described in detail (León and Oesterheld, 1982; Oesterheld and León 1987). These authors studied changes in floristic composition, plant soil cover and specific productivity, finding that in a 15–18-year period the community recovers almost all of its original species and the dominance of *Stipa charruana*. Yet there is still very little information on how pasture planting may affect the structure of the grassland communities as a consequence of alterations in soil–plant relationships and plant-to-plant interactions. Tilling causes dramatic changes in the physical and chemical properties of the topsoil. Layers with different pH, salt and organic matter contents are mixed, and tilling machinery produces soil compaction, that may be aggravated later by cattle trampling. Flooding may revert some of these changes in soil properties, and this reversion is followed by the secondary succession that operates once tilling of the soil disappears (Lavado et al. 1992; Chaneton et al. 2002). Changes in the successional pathways initiated by opportunistic pasture planting may induce important changes in nutrient and water cycle within the ecosystem, strongly modifying its properties (Wedin 1995; Wedin and Tilman 1996; Quinos et al. 1998).

In this study we made field surveys in natural grasslands and very old pastures, using transects located across existing topographic gradients, in order to document the changes caused by cultural activities on the structural and functional characteristics of the plant communities in a landscape of the Flooding Pampa grassland. We expect that opportunistic pasture planting will expand the narrow ecotones separating patches of the natural grassland, which make apparent the discrete limits between stands of the different communities. Therefore, the natural patchy pattern of the grassland will change into a vegetation gradient following the small topographic differences, especially reducing the compositional and functional heterogeneity of the vegetation at landscape scale.

Characteristics of the landscape

The landscape of the area is made up of the divides, slopes and bottoms of watersheds of the tributaries of the Samborombon River in the northern portion of the Flooding Pampa (León et al. 1979), with slopes of less than 0.1% and lying between 10 and 20 m a.s.l. These flat, extensive divides and slopes present an intricate mosaic of three landscape elements (Figure 1) with height differences no greater than 0.30 m, each with differing soil characteristics and plant communities. These elements are: (1) positive areas (60% of the total surface); (2) flat, depressed areas (30%) and (3) negative, concave, elongated areas (microchannels) (10%). The soils of the positive areas are typic paleudols or typic cromuderts; in the lower negative areas, aquentic cromuderts and typic natracualfs are dominant, while on the flat areas, typic natracuols are predominant (INTA 1989). While the positive areas are rarely flooded, the other two elements of this pattern get waterlogged during winter and early spring. The vegetation changes according to these soil and topographic characteristics of the landscape. Four different plant communities are found: *Stipa charruana*–*Cynara cardunculus*–*Borreria dasycephala* (a mesophytic prairie), or *Stipa papposa*–*Stenotaphrum secundatum*–*Distichlis* spp. (a humid mesophytic prairie) communities on the higher parts of the landscape; *Sporobolus pyramidatus*–*Nostoc* sp.–*Sporobolus indicus* community (an halophytic steppe) on the flats and *Althernantera philoxeroides*–*Mentha pulegium* community (a meadow) on the depressions (León et al. 1979; Perelman et al. 2001).

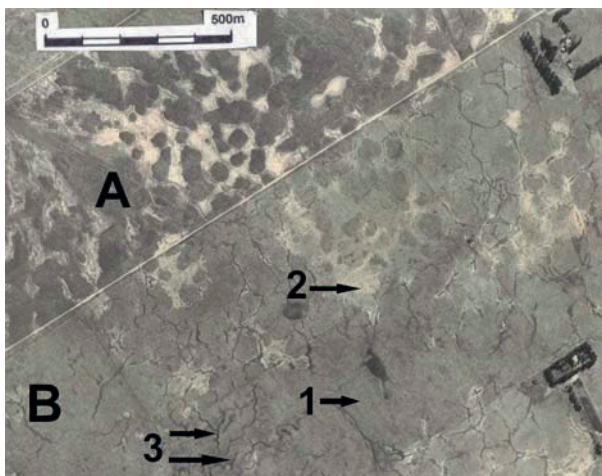


Figure 1. Airphotograph of the studied landscape showing its elements and their arrangement. A: recently tilled field; B: grassland. 1: positive areas, 2: flat, depressed areas, 3: concave micro-channels.

Materials and methods

We selected five pairs of neighboring fields, where each pair consisted of a field of natural grassland and an old pasture. A transect encompassing the entire topographic gradient of each field was located to sample vegetation. Along each transect, samples were taken systematically every 20 m, resulting in 6–9 samples per transect (totalizing 38 samples in natural grasslands and 33 in old pastures). Each vegetation sample consisted of a complete list of the vascular plants present, and an estimate of species cover within an area of 10×2 m located perpendicular to the transect. Sampling was carried out in early summer, when most species are present and easily identifiable through their reproductive organs.

In order to determine and describe the variation in species composition across sites in both, old pastures and grasslands, we classified them in vegetation units by means of a fusion algorithm, which resulted from Sorensen distance measures (Digby and Kempton 1987) used to calculate the farthest neighbor clustering from presence–absence data of all species present in more than 2 samples: 92 species in old pastures and 96 species in grasslands. The frequency (constancy) and the average cover of each species were compared for old pastures and grasslands within vegetation units.

We studied the principal gradients in species composition and compared the amount of habitat heterogeneity present in tilled and non-tilled grasslands with correspondence analysis (Greenacre 1984), applied on the complete matrix of cover data encompassing pastures and grasslands (127 species with presence greater than 2 in the complete inventory = 71 sampling units). Both, for classification and ordination, cultivated pasture species (*Festuca arundinacea*, *Thinopyrum ponticum*, *Dactylis glomerata*, *Phalaris aquatica*) were excluded from the analysis.

We explored the proportional contribution of different plant functional types that may be indicators of changes in ecosystem processes as a result of opportunistic tilling, such as biological invasions or production seasonality: exotics vs. natives, annuals vs. perennials, cool-season vs. warm-season species, testing the hypothesis of homogeneity between grassland and old-pastures within each environment. We applied Fisher exact probability test (Weerahandi 1995) to determine whether each pair of sites differ, significantly, in the proportion of species belonging to each functional group. We estimated average number of species per sample, total number of species and rate of species turnover (beta diversity = total number of species per site/mean number of species per site, Magurran 1988) for the two groups of samples. For each grassland community, we determined the percentage of exclusive species lost in relation to total number of exclusive species for that community. For each old-pasture community, we counted the number of species gained according to their origin, considering ‘species new to the landscape’ all those not present in the grassland communities and ‘from other communities’ the rest of species gained. We also calculated beta turnover for each grassland community as

(number of species gained + number of species lost)/(total number species in grassland + total number species in old pasture) (Shmida and Wilson 1985). For each transect, we calculated Jaccards percentage similarity index (Digby and Kempton 1987) between sites located at the extreme topographic positions. We compared the average of these values between grassland and old-pasture sites with a *t*-test. Finally, we built a species–area curve for each transect by calculating the cumulative number of species as area increased. Then we averaged the species area curves for old pasture transects and for grassland transects, respectively.

Results

The correspondence analysis revealed the floristic heterogeneity of this grassland, determining four clusters that correspond to four plant communities and confirms the patchy structure of this landscape (Figure 2, Table 1). The two most similar clusters include the stands of the well-drained soil: (G1) associated with the habitat offered by the convex highest topographic positions of the landscape and (G2) constrained to the similar but relatively lower positions. Noteworthy, richness in (G1) is greater than in (G2), which lacks 33 species (Table 2a) including a native shrub (*Baccharis spicata*), some sub-shrubs (*B. pingrae*, *Margiricarpus pinnatus*, *Sida rhombifolia*, *Vernonia rubricaulis*), and some exotic weeds, such as thistles (*Cynara cardunculus*, *Carduus acanthoides*, *Cirsium vulgare*). The other two clusters correspond to the stands

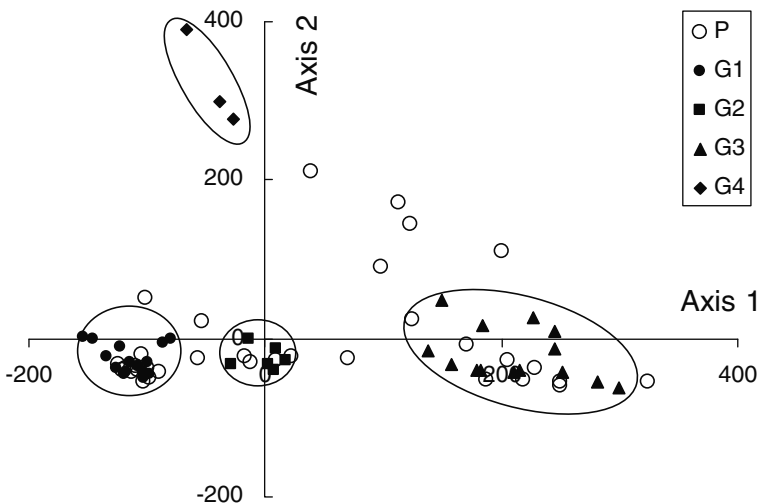


Figure 2. Correspondence analysis: the clusters correspond to four grassland communities. Old pastures sample-points are superimposed and scattered in-between the grassland clusters, the upper extreme along axis 2 missing.

Table 1. Partial ordered constancy table for grasslands (G) and old pastures (P) in the different vegetation units: MP= mesophitic prairie, HMP=humid mesophitic prairie, HS= halophytic steppe, M= meadow.

ES	Gained		Vegetation unit Community Species/No. samples	MP		HMP		HS		M	
	NL	GC		G1	P1	G2	P2	G3	P3	G4	P4
1*			<i>Asclepias mellodora</i>	27							
1*			<i>Calotheca brizoides</i>	7							
1*			<i>Chevreulia acuminata</i>	7							
1*			<i>Teucrium cubense</i>	7							
1*			<i>Torilis nodosa</i>	7							
			<i>Carex bonariensis</i>	20				7			
1*			<i>Panicum sabulorum</i>	13							
1			<i>Bromus hordeaceus</i>	53	30						
1			<i>Taraxacum officinale</i>	13	10						
1			<i>Baccharis coridifolia</i>	20	10						
1			<i>Bromus catharticus</i>	20	10						
1			<i>Medicago lupulina</i>	47	30						
	1		<i>Crepis setosa</i>		10						
	1		<i>Digitaria sanguinalis</i>		10						
	1		<i>Oxalis conorrhiza</i>		10						
	1		<i>Scutellaria racemosa</i>		10						
	1		<i>Veronica arvensis</i>		10						
	1		<i>Centaurea jacea</i>		30						
	1		<i>Cichorium intybus</i>		20						
	1		<i>Melilotus albus</i>		20						
3*		1	<i>Eryngium elegans</i>		30			7			
1			<i>Paspalum notatum</i>	7	20						
1			<i>Sonchus asper</i>	7	20						
1			<i>Hypochaeris chillensis</i>	7	30						
1			<i>Trifolium repens</i>	13	30						
1			<i>Trifurcia lahue</i>	13	40						
1			<i>Lactuca serriola</i>	7	10						
1			<i>Margyricarpus pinnatus</i>	7	10						
2*			<i>Briza minor</i>			17					
2*			<i>Juncus dicothumus</i>			17					
2*			<i>Pfaffia gnaphaloides</i>			17					
2*			<i>Trichocline sinuata</i>			17					
2*			<i>Richardia stellaris</i>			33					
			<i>Schizachyrium spicatum</i>	7		33					
2*		1	<i>Chevreulia sarmentosa</i>		10	17					
			<i>Leucanthemum vulgare</i>	20	40	17					
			<i>Stenotaphrum secundatum</i>	73	10	33		21			
			<i>Cyperus eragrostis</i>	13		17					
			<i>Cuphea glutinosa</i>	13	10	17					
			<i>Baccharis trimera</i>	33	30	17	11				
			<i>Centaurea calcitrapa</i>	53	30	17	22				
			<i>Piptochaetium stipoides</i>	53	20	33	44				
			<i>Verbena montevidensis</i>	87	80	33	67				

Table 1. (Continued)

ES	Gained		Vegetation unit Community Species/No. samples	MP		HMP		HS		M	
	NL	GC		G1	P1	G2	P2	G3	P3	G4	P4
			<i>Piptochaetium bicolor</i>	80	80	67	44				
			<i>Jaegeria hirta</i>	33	40	17	11				
1		2	<i>Cynara cardunculus</i>	53	30		11				
1		2	<i>Melica brasiliana</i>	73	30		11				
1		2	<i>Convolvulus hermanniae</i>	7	60		22				
1		2	<i>Physalis viscosa</i>	13	70		33				
1		2	<i>Anagallis arvensis</i>	7	30		22				
1		2	<i>Cirsium vulgare</i>	47	70		22				
1		2	<i>Briza subaristata</i>	13	10		11				
1		2	<i>Conyza blakei</i>	73	40		67				
1		2	<i>Carduus acanthoides</i>	87	80		67				
1		2	<i>Vernonia rubricaulis</i>	33	20		33				
1		2	<i>Sida rhombifolia</i>	87	90		11				
1		2	<i>Ammi majus</i>	67	90		56				
1		2	<i>Baccharis pingraea</i>	13	20		11				
1		2	<i>Solidago chilensis</i>	13	20		11				
1		2	<i>Borreria dasycephala</i>	80	90		33				
	2		<i>Hirschfeldia incana</i>				11				
	2		<i>Polygala australis</i>				11				
1*		2	<i>Baccharis spicata</i>	7			44				
	2		<i>Avena sp.</i>				22				
	2		<i>Oenothera parodiana</i>				22				
1*		2	<i>Glandularia peruviana</i>	7			33				
1*		2	<i>Wahlenbergia linarioides</i>	7			33				
1*		2	<i>Apodanthera sagittifolia</i>	7			11				
	1,2		<i>Dactylis glomerata</i>		30		44				
	1,2		<i>Phalaris aquatica</i>		60		78				
	1,2		<i>Trifolium pratense</i>		20		56				
	1,2,3,4		<i>Festuca arundinacea</i>		80		22		22		20
	1,2,3,4		<i>Thinopyrum ponticum</i>		70		22		78		60
	1,2,3		<i>Nicotiana longiflora</i>		10		11		11		
		2	<i>Stipa charruana</i>	87	40		11	29	33		
		2	<i>Cynodon dactylon</i>	7	50		22	14	11		
2		1,4	<i>Silene gallica</i>		10	17	22				20
	3		<i>Medicago polymorpha</i>						11		
	3		<i>Portulaca oleracea</i>						33		
			<i>Aristida murina</i>	40		100	22	21			
			<i>Noticastrum diffusum</i>	27		33	11	21			
			<i>Carthamus lanatus</i>	53	40	33	22	7	11		
			<i>Gaudinia fragilis</i>	33	40	17	22	29	33		
		3	<i>Cyclopernum leptophyllum</i>	73	80	33	56		11		
			<i>Vulpia myuros</i>	60	20	50	11			33	
			<i>Hypochaeris radicata</i>	80	70	17	22			33	20
1		4	<i>Jaborosa integrifolia</i>	7	20						20

Table 1. (Continued)

ES	Gained		Vegetation unit Community Species/No. samples	MP		HMP		HS		M		
	NL	GC		G1	P1	G2	P2	G3	P3	G4	P4	
				15	10	6	9	14	9	3	5	
1	4		<i>Oxypetalum solanoides</i>	40	70						20	
	4		<i>Adesmia bicolor</i>	47	70	50	67				20	
	4		<i>Conyza primulifolia</i>	53	20	33	22				20	
	4		<i>Dichondra microcalyx</i>	87	50	33	56	7			20	
			<i>Grindelia discoidea</i>			67	44	64	44			
			<i>Spergula villosa</i>			17	11	14				
			<i>Cypella herberti</i>	33	10	67		7			33	40
			<i>Eryngium echinatum</i>	27	40	50	44	29			67	60
			<i>Juncus imbricatus</i>	67	60	67	11	36			33	40
			<i>Sisyrinchium platense</i>	7		33	33	36			33	20
			<i>Leontodon taraxacoides</i>	7	20	33					67	20
			<i>Mentha pulegium</i>	33	20	17	22				100	20
		2		<i>Aster squamatus</i>	13	30		33	14		100	60
				<i>Agalinis communis</i>	13	20	50	11			67	20
				<i>Panicum hians</i>	33	40	50	22	14	22	67	40
				<i>Phyla canescens</i>	100	80	83	56	7	22	67	60
				<i>Lotus glaber</i>	93	100	100	100	36	33	100	80
				<i>Centaureum pulchellum</i>	87	100	100	89	43	11	33	20
				<i>Sporobolus indicus</i>	20	30	100	33	86	44	33	80
				<i>Paspalum distichum</i>			17	11	14	22	33	40
				<i>Cyperus corymbosus</i>	27	10	50	33	14	33	33	80
				<i>Acemella decumbens</i>	13	40	33	78	43	44	67	80
				<i>Paspalum dilatatum</i>	93	100	33	33	7	33	33	40
				<i>Lolium multiflorum</i>	73	80	50	78	21	11	67	60
				<i>Setaria parviflora</i>	60	70	83	89	21	22	33	60
		4		<i>Conyza bonariensis</i>	53	60	50	56	14	22		20
		4		<i>Stipa papposa</i>	73	60	83	33	86	67		20
		4		<i>Piptochaetium montevidense</i>	33	30	67	67				20
		4		<i>Berroa gnaphalioides</i>	60	40	83	22	14	22		40
		4		<i>Eragrostis lugens</i>	13	30	83	78	14	67		20
		4		<i>Gamochoeta</i> sp.	33	60	67	56	14	11		20
		4		<i>Plantago myosurus</i>	7	50	50	22	43	22		20
		4		<i>Stipa neesiana</i>	53	70	83	78	7	44		20
		4		<i>Pterocaulon virgatum</i>	60	50	100	78	71	89		60
		4		<i>Panicum bergii</i>	33	40	67	56	57	56		40
		4		<i>Ambrosia tenuifolia</i>	80	80	100	100	50	78		40
	3,4		<i>Bothriochloa laguroides</i>	100	100	100	22		11		20	
	4		<i>Nostoc</i> sp.			50		93	100		60	
	4		<i>Chloris berroi</i>			50	56	79	100		60	
	4		<i>Spergula laevis</i>			33	33	29	44		40	
	1,4		<i>Eleusine tristachya</i>		10	33	22	29	78		20	
	1,4		<i>Chaetotropis elongata</i>		10			21			40	
	4		<i>Distichlis scoparia</i>			33		57	100		60	
3	2,4		<i>Distichlis spicata</i>				11	57	11		20	

Table 1. (Continued)

ES	Gained		Vegetation unit Community Species/No. samples	MP		HMP		HS		M	
	NL	GC		G1	P1	G2	P2	G3	P3	G4	P4
3		2,4	<i>Sporobolus pyramidatus</i>					11	100	100	40
1		3,4	<i>Juncus capillaceus</i>	13	10					11	20
		2,4	<i>Juncus microcephalus</i>	7	10			11	7		20
3		2,4	<i>Diplachne uninervia</i>					11	43	11	60
		1	<i>Paspalum vaginatum</i>		10				14	22	33
3			<i>Puccinellia glaucescens</i>						21	44	
3			<i>Lepidium parodii</i>						21	22	
3			<i>Solanum elaeagnifolium</i>						21	22	
3		4	<i>Lepidium spicatum</i>						36	78	40
			<i>Pappophorum philippinianum</i>			33			64	67	
3		2	<i>Acicarpa procumbens</i>				22		21	22	
3*			<i>Senecio pinnatus</i>						50		
3*			<i>Petunia parviflora</i>						14		
3*			<i>Spergula ramosa</i>						7		
3*		4	<i>Hordeum stenostachys</i>						36		20
4*			<i>Bromidium hygrometricum</i>								67
4*			<i>Echinochloa</i> sp.								33
4*			<i>Glyceria multiflora</i>								33
4*			<i>Juncus</i> sp.								33
4*			<i>Marsilea ancylopoda</i>								33
4*			<i>Roripa bonariensis</i>								33
4*			<i>Rumex</i> sp.								33
4*			<i>Gratiola peruviana</i>								100
			<i>Nothoscordum gracile</i>	7							33
			<i>Stipa philippii</i>	7							33
4			<i>Alternanthera philoxeroides</i>								100
			<i>Eleocharis</i> sp.	7							100
4			<i>Leersia hexandra</i>								67
		2	<i>Eryngium ebracteatum</i>	40			11				100
4			<i>Danthonia montevidensis</i>								33
4			<i>Pamphalea</i> sp.								33
4			<i>Stipa formicarum</i>								33
		4	<i>Centella asiatica</i>								20
3*		4	<i>Acicarpa tribuloides</i>						14		20
		2,4	<i>Sida spinosa</i>				11				20

ES: species exclusive to one grassland community,* exclusive species lost.

NL: species gained, new to the landscape, GC: species gained from other communities. Values are constancy (% frequency) in each community. Nomenclature follows Zuloaga et al. (1994), Zuloaga and Morrone (1996, 1999).

occupying the topographic sites with waterlogged-prone soils: (G3) found in the less frequently flooded, saline-alkaline soils habitat, which is characteristic of the mild topographic gradient between uplands and lowlands, and (G4) with the least species richness (Table 2a), distributed on the lowest topographical positions and small channels. In the old pastures, sample-points are

Table 2. Species gained or lost in: (a) the grassland communities; (b) the old pastures.

(a)				
Grassland community	G1	G2	G3	G4
Total number of species	99	66	60	39
Number of exclusive species	40	7	14	13
Number exclusive species lost	10	6	6	8
% exclusive species lost	25	86	43	61
(b)				
Old pasture community	P1	P2	P3	P4
Species gained from other communities	6	28	3	32
Species gained, new to the landscape	14	11	5	2

superimposed and scattered in-between the original grassland clusters, generally displaced downwards and with the upper extreme along axis 2 missing (Figure 2). Both, the grassland communities (G1, G2, G3 and G4) and the corresponding old pastures (P1, P2, P3 and P4) had differences in their species composition (Table 1). G4 sites had the greatest difference with the other grassland communities, with an average similarity of species lists equal to 0.36. The corresponding old pasture (P4) instead, becomes more similar to the old pastures of the other environments with an average similarity of 0.57.

There are 74 species exclusive to anyone of the grassland communities, while only 48 exclusive to anyone of the old pastures. As a result of tillage, the different grassland communities lost an important number of their exclusive species, but also gained species, some new to the landscape while others were already present in the other environments (see Table 2 for total numbers and Table 1 for species identity). The grasslands from the intermediate and lower topographical positions (G2 and G4) lost the most of their exclusive species (86 and 61%, respectively, Tables 1, 2a) and were the ones that gained most species (38 and 34 species, respectively, Table 1). The sites of the richest community (G1) gained the highest number of species new to the landscape, while the one from the poorest (G4) was enriched mainly by species from the landscape species pool (Tables 1, 2b). A total of 20 species were gained in the landscape: 35% of them were established in more than 1 community and 14 species colonized the sites of the better drained soils (G1) (Table 1).

Other species had different behaviors in response to tilling and pasture planting. Some, generally having greater constancy values than the exclusive species to each of the grassland habitats, were still present in the old pastures, but had constancy values ca. 50% lower than in the untilled fields. *Cynara cardunculus*, *Melica brasiliensis* and *Conyza blakei* are within the species that appear to have some sensitivity to pasture establishment, but their constancy reduction was partially compensated for by their presence in the new habitats created by the cultural practices in the formerly G2 stands (P2, Table 1). *Stipa charruana*, a native, dominant grass was distributed along a wider range of environments than the previous set of species, as it also occupied the habitats of the lower topographic stands with less drained soils (G3, Table 1). Cultural

practices for pasture planting reduced by 46% the constancy value for this coarse, perennial grass, only in the convex well-drained soil habitats (G1 vs. P1, Table 1). This reduction, as in the case of other species, was partially compensated for by its occurrence in P2 cultural habitats, located in the intermediate topographic sites, where it was originally absent (G2).

Numerous species disappeared as a consequence of the disturbance. For example, *Sisyrinchium platense*, *Chaetotropis elongatus*, *Stenotaphrum secundatum* and *Eryngium elegans* present in G3, are absent in P3. A number of constant species (*Althernantera philoxeroides*, *Leersia hexandra*, *Eryngium eb-racteatum*, *Danthonia montevidensis*, *Pamphalea bupleurifolia* and *Stipa formi-carum*) present in G4 decreased their constancy in P4. On the other hand, after pasture planting in G1 stands, five species increase their constancy (*Paspalum notatum*, *Sonchus asper*, *Trifolium repens*, *Hypochaeris chilensis*, *Trifurcia la-hue*) and only three decrease (two *Bromus* species and *Medicago lupulina*). Despite the important changes in species composition that resulted from pasture planting, comparisons of plant functional types among the various grassland communities and with the corresponding old pastures yielded no significant differences (Figure 3).

On average, total plant cover of grasslands and old pasture sites was ca. 70% (Figure 4). In both cases, the sites of the higher topographic positions had the highest cover, while the waterlogged and halomorphic sites, the lowest. In sites of intermediate topographic positions, the cover data from the grassland stands had less variability than those from the old pastures. Therefore, despite of the similarity in cover values (G2 = 76%, G4 = 62% and P2 = 72%, P4 = 59%), statistical differences ($p = 0.005$) between higher and lower positions appeared only for grasslands (Figure 4).

At a more detailed scale, pasture planting reduced the rate of species replacements along the studied topographic gradient, since the floristic similarity between contiguous samples was greater in the old-pastures than in the grasslands (Figure 5). However, despite the changes in patchiness, the species–area curve (Figure 6) at landscape scale was not affected. Neither did we find differences between grasslands and old-pastures in total number of species (G = 146; P = 140), average number of species/site (G = 27.9; P = 29.1) and beta diversity (G = 5.2; P = 4.8).

Discussion

The characteristic structure of the grassland communities of this flat intricate landscape is patchy, with well-defined stands corresponding to important edaphic differences that follow the existing subtle relative topographic variation. Soil tilling and pasture planting erased the defined boundaries separating these stands and generated a vegetation gradient. Probably, a great part of this change is caused by tilling operations, which flattens the convex patches as well as the small channels, mixes the organic matter and salts of the surface soil

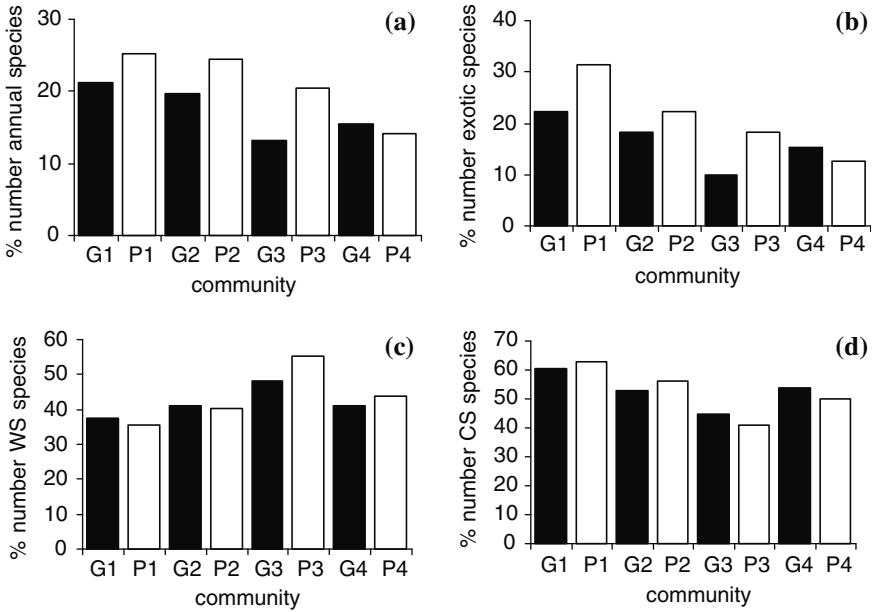


Figure 3. Percentage number of species corresponding to the different functional types yielded no significant differences for grasslands and old pastures: (a) annual species, (b) exotic species, (c) warm-season species, (d) cool-season species.

accumulated in the different layers, distributing them rather homogeneously within the plowed profile. Alien species to the landscape appeared in the cultural habitats created by pasture planting, which included not only the sown forage species, but also some weeds and natives to the region (Chaneton et al.

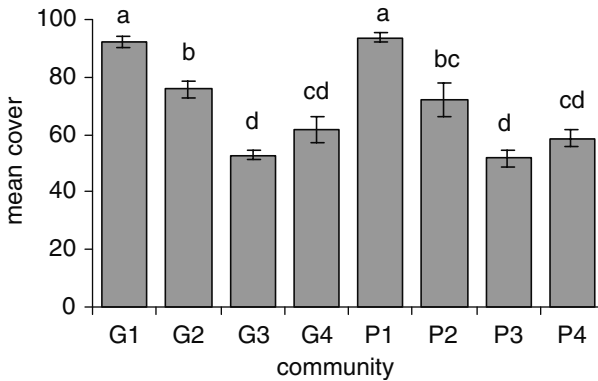


Figure 4. Percentage total plant cover for each grassland and old-pasture community. Vertical bars are standard errors. Different letters represent significant differences between mean values ($p < 0.05$).

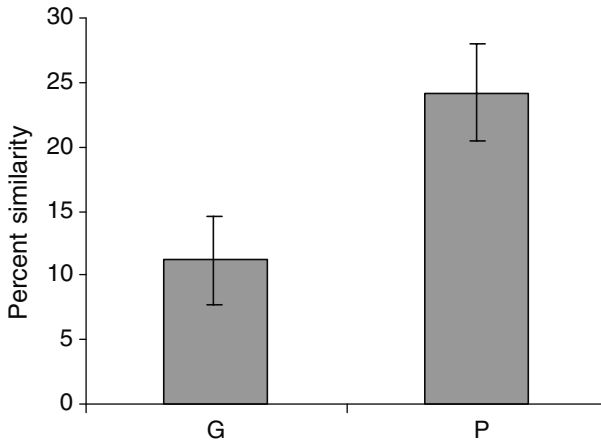


Figure 5. Floristic similarity between contiguous samples (Jaccard Similarity Index) for grasslands and old pastures.

2002). The new grasslands (P) created by the old-pastures had less structural differences along the topographic gradient than the original ones (G). The mesophytic meadows (G1) and the hallophytic steppe (G3) gained mainly species new to the landscape (70 and 62%, respectively) while in the humid mesophytic prairies (G2) and meadows (G4) more than 70% of the incoming species belonged to the regional species pool (70 and 94%, respectively). All communities lost at least 25% of their exclusive species, the humid mesophytic prairies (G2) losing the most (86% of exclusives). The exclusive species that expanded their distribution ranges did so to two or three of the communities of old pastures.

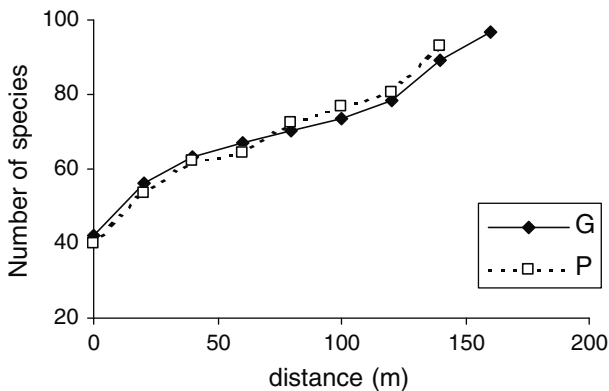


Figure 6. Species-area curves for grasslands and old-pastures at landscape scale were not affected despite changes in patchiness.

Opportunistic pasture planting produced the least impact in the patches of better drained soils covered by mesophytic prairies (G1, beta turnover = 20%), as accounted by losing 25% of its exclusive species group, and by the addition of 20% of new species, (14% alien to the landscape and 6% redistributed within the landscape), relative to the total of 99 species. It is the richest community and it contributed to 40% of the species redistributions that occurred within the patches of the landscape as a consequence of pasture plantings. As shown for other ecosystems (Levine and D'Antonio 1999; Lonsdale 1999; Stohlgren et al. 1999), in these grasslands it is also the richest community the one that gains the highest number of species. Forty three percent of G3 exclusive species were lost in the old pasture stands (P3), and were replaced by the invasion of 8 species, yielding an overall 25% (beta turnover) change, compared to its 60 total species number.

G2 stands that were turned into old pastures increased by 35% their species richness (from 66 to 89 species) and lost 86% of its exclusive species. They underwent a floristic change amounting to 35% (beta turnover value) of its average list (72% of gained species belong to species redistributed within the landscape patches). Seventy seven percent of the species that came to P2 through local species redistribution belonged to G1, indicating that whatever ecological factor/s, biotic or not, curtailing G1 species from expanding their ranges into G2 sites, which occur at subtle topographic differences, disappeared. Contrarily only two species from G2 were able to expand their ranges into P1 environments. Tilling activities increased the floristic similarity of this community with the mesophytic prairie and with the meadows.

The greatest structural impact caused by opportunistic pasture planting occurred in G4 humid community of the grassland. These sites lost 61% of its exclusive species, and had 46% change in its floristic composition (beta turnover value) with 94% redistribution within the landscape. Half of the redistributed species that appeared in the P4 list were also in the G1 and G2 lists, but a significant number (60% of the redistributed species) also were shared with those in G3. Only two species gained by G4 are new to the landscape. This complex of species, fed by all the originally different communities of the landscape, was almost certainly caused by the mixture of soil layers resulting from soil tilling in the less drained lower topographic sites of the landscape, which created a small-grain heterogeneous soil mosaic that allowed the establishment of a diverse group of species. Despite the fact that flooding may revert some of the changes in soil properties caused by tilling, which is followed by a recovery of the original community (Lavado et al. 1992), the patches of the more humid communities surveyed in our study remained opened to the establishment and growth of the other habitat species, notwithstanding the several flooding events that have occurred since the old pastures planting time. It is interesting to point out that not a single species of G4 extended their distribution range to the P1, P2 and P3 cultural habitats. These floristic shifts, caused by immigrations to stands in different topographic positions along the gradient, and local extinctions, could be induced by habitat changes due to

pasture planting, but also related to species sampling (Casagrandi and Gatto 1999; Hillerbrand and Blenckner 2002). For example, stands of the better drained soils (G1, G2) covered 60% of the landscapes area and thus, it would be expected that they gain most of the species new to the landscape and have few extinctions, as they did, while the microchannels covering only 10% of the area should have the greatest extinctions and least immigrations.

Chaneton et al. (2002) studied the effects of grazing on heterogeneity and alien plant invasion in the temperate grasslands of the Flooding Pampa. They concluded that grazing promoted exotic plant invasion and generally enhanced community richness, whereas it reduced the compositional and functional heterogeneity of vegetation at landscape scale. That means that grazing effects on floristic heterogeneity were scale dependant. Our data suggests that adding the soil-tilling disturbance to domestic animal grazing did not change the general pattern they described for grazing alone. Noteworthy, apart from the five forage species that were presumably sown into the original habitats and the other 17 that invaded into the landscape old pasture communities, most of the contributions to the patches species richness came from redistribution within the landscape habitats dominated by native species (60 species gained from other communities).

As it was shown by our results, several infrequent species, but with high fidelity to their community and therefore strongly fitted to particular habitats created by subtle topographic variations, appeared to be very sensitive to the ecological changes introduced by opportunistic pasture planting. Within this group, there are perennial grass species that are highly valuable for animal grazing, like *Calotheca brizoides* and *Panicum sabulorum*, and others, like *Asclepias mellodora*, which is one of the few native Asclepiadaceae found in the region that has flowers hosting a lepidopteran (*Danaus emipus*). Both, the showy flowers and the black and yellow larva of this butterfly, makes this species conspicuous in the stand. Exclusive species loss could alter the grassland functions, as the one just described, as well as others that are unknown because they are less conspicuous. Therefore, these losses should not be underestimated when discussing the overall impact of opportunistic pasture planting on the grassland communities.

Clearly the new grassland created by an opportunistic pasture planting has developed into a structural gradient in which the sites of the well drained soils experienced only small structural change (León and Oesterheld 1982; Oesterheld and León 1987) whereas important differences occurred in the lower waterlogged-prone stands. Some of the steppe species in the saline-alkaline patches of the original grassland were replaced by perennial forage and native species with autumn-winter-spring production peaks, while the community from the more humid acid soil patches was completely changed by the invasion of species from the rest of the habitats.

Plant cover differed only between grassland stands sampled in sites with intermediate positions of the landscapes topographic gradient (Figure 4). The increase in variability associated to pasture planting could be related to

differences in management of animal grazing that may have existed between grassland and old pasture fields, which were not controlled in our study. Nevertheless, because grass tussocks contributed the most to plant cover, we believe that other more stable structural changes, related to those factors affecting floristic composition of the old pasture stands were mostly responsible for cover variability (Figure 2, Table 1).

Implications for grassland conservation

The fine grain packaging of species diversity suggests that most of the heterogeneity at the species level could be conserved by establishing protected areas, although the minimum area needed to include a given amount of diversity may not necessarily be enough for its persistence (Perelman et al. 2001). As expected, opportunistic planting of pastures impacted mostly changing the patchy structure of the landscape by reducing its heterogeneity. This may be viewed by ranchers as an improvement for managing grazing of cattle (De León and Cauhepé 1988), yet it may have profound ecological impacts, especially on trophic webs (Bailey et al. 1996; De Vries et al. 1999; Hutchings et al. 2002; Braschler et al. 2003). A large proportion of the Flooding Pampa natural grassland communities are still preserved, but this situation is rapidly changing as the need to improve economic outputs, and availability of new technologies, enhance their replacement to pastures and annual crops. The landscape we studied in this work has an intricate patchiness and a soil type (vertisol, cromudert) that is only found in a relatively small area in the north of this region, which is near to the urban landscapes of the cities of La Plata and Buenos Aires. These characteristics draw attention to its importance for developing conservation activities as soon as possible, not only because of its uniqueness but also, because it is highly jeopardized by the expansion of human activities. Our study provides important information for taking decisions about conservation. On one hand, extensive grazing activity has to be preserved in order to curtail expansion of alternative land uses (Naveh et al. 2001), but most importantly, this activity has to be carried out avoiding soil plowing and pasture planting. Should the landscape's original intricate community pattern be preserved, expansion of soil tilling and pasture planting ought to be stopped. On the other hand, if aims are focused only on preservation of floristic richness, these agronomical practices have little impact.

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Decreased frugivory and seed germination rate do not reduce seedling recruitment rates of *Aristotelia chilensis* in a fragmented forest

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Abstract Habitat fragmentation reduces frugivorous bird abundance. Such a reduction may lead to a reduction in seed dispersal, thereby compromising seedling recruitment rate with far reaching consequences for plant population persistence. We assessed frugivory, seed germination, and seedling recruitment rates in a fragmented forest of central Chile by comparing a continuous forest with four forest fragments surrounded by pine plantations. Frugivory was 2.4 times higher in continuous forest than in forest fragments. Seeds eaten by birds germinated 1.7 and 3.7 times higher than non-eaten seeds from continuous forest and fragments respectively. Non-eaten seeds from continuous forest germinated 2.2 times higher than those from forest fragments, suggesting inbreeding depression. However, seedling recruitment rates at forest fragments were far higher than in continuous forest where no seedling recruited in the five years analysed. Therefore, despite forest fragmentation negatively affected frugivory, it did not translate into a decreased fitness of plants, thus highlighting the importance of considering the overall processes leading the reproductive success of plants following anthropogenic disturbances.

Keywords Forest fragmentation · Avian frugivory · Seed quality · Seedling recruitment rates

Introduction

Habitat fragmentation can have profound effects on frugivory and seed dispersal with negative consequences for plant fitness (Santos and Telleria 1994; Galetti et al. 2003; Şekercioğlu et al. 2004). The reduction in habitat size and increment in isolation can reduce the diversity and abundance of the remaining frugivores. Such reductions may lead

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to a reduction in the intensity of frugivory, and consequently, in seed dispersal and upon seedling recruitment (Galetti et al. 2003; Cordeiro and Howe 2001, 2003; Traveset and Riera 2005).

Small patches of fruiting plants may be less attractive to frugivores as they offer a lower food reward (Saracco et al. 2004). Because sugar concentration of pulp fruits depends on environmental conditions (Ito et al. 1999), forest fragmentation might then affect the attractiveness of plants to frugivores by increasing sugar concentration given the lower environmental humidity of forest fragments. Frugivores prefer concentrated pulps, which may in turn trigger an increased frugivory rate (Stanley et al. 2002). Because habitat fragmentation reduces atmospheric humidity (Camargo and Kapos 1995), the attractiveness of fruits, in terms of sugar concentration, might be higher in fragmented populations. Therefore, habitat fragmentation could lead to contrasting tendencies: a reduction of frugivory, since small and isolated patches are less attractive and harbour a depauperated fruit-feeding animal abundance; or increased frugivory rates, because fruits in fragments might produce more concentrated pulps, leading to some sort of compensation, or even overcompensation, of the lowered population sizes, and hence similar rates of frugivory in continuous forests and forest fragments.

A failure in seed dispersal triggered by a lowered frugivory might lead to a clumped pattern of tree recruitment which may in turn favour a higher mating ratio among close relatives (Bleher and Böhning-Gaese 2001). Therefore, failures in frugivory coupled to a reduction in plant population size and increased isolation triggered by habitat fragmentation may lead to inbreeding depression (Barrett and Khon 1991; Young et al. 1996). Inbreeding depression in turn, may produce a reduction in seed quantity i.e., seed per fruit) and seed quality (i.e., germination rate) (Barrett and Khon 1991; Young et al. 1996; Henríquez 2004). Certainly, the reduction in frugivory coupled to the lowered fitness of plants in terms of the seed quality and quantity may reduce the seedling recruitment rates, which might compromise the long-term population persistence (Barrett and Khon 1991; Galetti 2003).

Although frugivorous vertebrates are rather scarce in the temperate rainforests of southern Chile, the proportion of vertebrate seed dispersal is roughly comparable to tropical forests (Armesto and Rozzi 1989; Willson 1991). In these temperate forests, birds are the most important frugivores being more than three-quarters of the whole vertebrate dispersers (Willson 1991; Aizen et al. 2002). Therefore, changes in frugivorous birds may lead to a changes in frugivory.

Currently, the southern temperate rainforest is severely fragmented which may affect animal-dispersed plants (Bustamante and Castor 1998; Bustamante et al. 2005). In these forests, assessments on the effects of forest fragmentation on birds have only recently been considered, reporting negative effects on richness and abundance of fruit-feeding birds (e.g., Willson et al. 1994; Vergara and Simonetti 2004). Despite this fact, however, there is a great knowledge vacuum concerning the potential effects of such reductions on seed dispersal and seedling recruitment rates. Here, we assess the effect of forest fragmentation on avian frugivory, seed quality, and seedling recruitment rates on the bird-dispersed tree *Aristotelia chilensis* (Elaeocarpaceae), a broadly distributed understory tree in temperate forest of southern South America (Rodríguez et al. 1983). If forest fragmentation negatively affect the frugivorous assemblage, we expect a negative effect on frugivory at the forest fragments with regard to continuous forest. Similarly, because forest fragmentation may also negatively affect seed quality, we expect a lower germination rate of seeds from forest fragments than from continuous forest. Therefore, because we expect a lowered seed dispersal rate coupled to a lowered seed quality, it is reasonable to expect a lowered seedling recruitment rate in fragments than in the continuous forests.

Materials and methods

Study site and species

The study was conducted in Maulino forest in the northernmost zone of the Southern temperate rainforest (35°59'S, 72°41'W; San Martín and Donoso 1996). Specifically, we worked in Los Queules National Reserve and four neighbouring forest fragments. Distance between continuous forest and fragments, and between fragments, ranges from 1 to 4 km (see Donoso et al. 2003 for a map). Los Queules is a protected area of 145 ha embedded in a large tract of 600 ha of continuous forest. Forest fragments, ranging from 1 to 6 ha, are patches surrounded by commercial plantations of *Pinus radiata*. Both in the forest fragments and in the continuous forest composition and abundance of adult trees are similar, the most abundant trees being *Aetoxicon punctatum*, *Cryptocarya alba*, *Gevuina avellana*, and *Persea lingue* among others (Bustamante et al. 2005).

Aristotelia chilensis (Elaeocarpaceae) is a dioecious tree of up to 4 m tall that inhabits the southern temperate rainforests (Rodríguez et al. 1983). While the adult abundance is roughly the same at both continuous forest and forest fragments, seedling abundance is higher at forest fragments (Bustamante et al. 2005). It bears black-coloured fleshy berries which are eaten and dispersed by fruit-feeding birds. Fruiting occurs from October to December, while fruit ripeness and seed dispersal occur from mid-December to January in the austral spring-summer season (Rodríguez et al. 1983). In the Maulino forest, potential dispersers are *Anairetes parulus*, *Elania albiceps*, *Xolmis pyrope* (Tyrannidae), *Aphrastura spinicauda* (Furnariidae), and *Turdus falklandii* (Muscicapidae) (Vergara and Simonetti 2004). In the study site, *A. parulus*, *E. albiceps* and *X. pyrope* are less abundant in forest fragments than in continuous forest, whereas *A. spinicauda* and *T. falklandii* are equally abundant in both forest fragments and continuous forest (Vergara and Simonetti 2004; González-Gómez 2004).

Fruit characteristics

To determine fruit characteristics, in January 2002, we randomly selected trees and branches and then collected ripe fruits ($n=30$ fruits from six trees in the continuous forest, $n=35$ fruits from six trees in the forest fragment, 1–2 trees per fragment) for assessing fruit size, quantity of seeds, and sugar concentration. Fruit size was estimated as the diameter of each fruit, while sugar concentration (mass percentage) was assessed with a hand-held temperature-compensated refractometer. All measurements were made in fresh fruits immediately after being collected.

Frugivory

The intensity of frugivory was experimentally assessed. We mimicked fruits making red-coloured wire branches bearing nine black-coloured plasticine fruits ($n=96$ branches with 864 fruits placed in the continuous forest, $n=100$ branches with 900 fruits in the forest fragments). The artificial infructescences were attached to individual fruiting trees (2–8 wire branches per tree depending on tree size; $n=16$ trees at continuous forest, $n=16$ trees at forest fragments, four per fragment) leaving them for the action of fruit-feeding birds during 30 days, from December 2001 to January 2002, coinciding with the period of seed dispersal. The only dispersers known for *A. chilensis* are fruit-feeding birds; hence, fruits

removed from infructescences were considered as dispersed by frugivorous birds, assumption reinforced by bill impressions on the picked fruits. This experimental array, mimicking natural infructescences of *A. chilensis*, allowed for a control of numerous traits which might otherwise bias the fruit-feeding animal choice, and thus the effect of forest fragmentation on frugivory (see Alves-Costa and Lopes 2001 on methodological details).

Seed germination

To determine the effect of consumption on seed germination, we placed for germination seeds randomly collected in January 2002 from faeces placed on the ground in the continuous forest and forest fragments ($n=150$ seeds from ca. 100 faeces), together with seeds collected from ripe fruits on trees ($n=150$ seeds from six trees in the continuous forest, and $n=150$ seeds from six trees in the forest fragments, 1–2 trees per fragment). This experimental design allowed to assess the effect of frugivores (eaten versus non-eaten seeds) as well as the origin of seeds (continuous forest versus forest fragments) on the seed germination rate.

Germination trials were carried out through a common garden experiment. Because we were incapable of assigning bird-eaten seeds to a specific site, they were only considered as dispersed seeds with mixed origin (i.e., from both continuous forest and forest fragments), thereby rendering conservative the comparisons with non-dispersed seeds from both types of sites. Seed germination was carried out during 250 days by placing 10 seeds from all individual trees into Petri capsules ($n=15$ capsules per treatment) placed inside germination chambers. Photoperiod of germination chambers was 12-h day/12-h night throughout all time of seed germination, whereas the temperature was modified according to the month when germination naturally occurs, thus mimicking natural conditions for germination (monthly temperature from March to November: 13.3, 10.9, 9.7, 8.5, 8.6, 8.8, 10.6, 12.3, and 13.6°C). Seeds were weekly irrigated with water. We considered a seed as germinated when the emerged root presented 2 mm elongation.

Seed rain and seedling recruitment rates

Forty seed traps were erected within the continuous forest, while other 40 seed traps were placed in forest fragments (10 at each fragment). Each trap consisted of a 0.25 m², open-topped, 1 mm wire-mesh bag held 0.8 m above the ground on a PVC frame. All seeds falling into the traps were counted and identified to the species level each month from January 2002 to December 2002. Because we were incapable of determining if seeds corresponded to bird-dispersed seeds or not, they were only considered as seed rain remaining the dispersal mechanism unknown.

To assess seedling recruitment rates we randomly placed plots of 2 m² ($n = 20$ in the continuous forest, and 20 in forest fragments, five per fragment). In these plots, we registered all woody plant less than 50 cm height (hereafter seedlings). Each seedling was individually tagged and identified to the species level from 1998 to 2004. Sampling was performed in September of each year, and survivors were recorded in January of the next year for registering all new recruits of the same recruitment season.

At both continuous and forest fragments, we placed two seed traps 2-m away from each plot. Thereafter, each plot and its two adjacent seed trap constituted a census station. Census stations were roughly linearly arranged at each site. The average distance (± 1 SE) from each census station to the next census station was 21.13 \pm 2.14 m at continuous forest,