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UNDERSTANDING FOREST-GRASSLAND MOSAICS: THREE CASE STUDIES ON THE BASALTIC PLATEAUS IN HUMID SUBTROPICAL BRAZIL

ANALIZANDO MOSAICOS DE BOSQUES Y PASTIZALES: TRES CASOS DE ESTUDIO EN EL SUBTROPICO HÚMEDO DE BRASIL

Marcela Pinillos[1,2],Guillermo Sarmiento[2], Lászlό Orlóci[3,4], Valerio D. Pillar[3]

[1]Programa de Pós-graduação em Ecologia, Universidade Federal de Rio Grande do Sul, Avenida Bento Gonçalves 9500, Porto Alegre 91540-000, Brazil. E-mail: marcela.pinillos@yahoo.com.ar
[2]Instituto de Ciencias Ambientales y Ecológicas (ICAE), Facultad de Ciencias, Universidad de Los Andes, Mérida 5101, Venezuela. [3]Laboratório de Ecologia Quantitativa, Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, Porto Alegre 91540-000, Brazil
[4]Department of Biology, University of Western Ontario, London, N6A 5B7, Canada.

ABSTRACT

Landscapes exhibiting complex mosaics of contrasting natural ecosystems, like forests and grasslands, continue to evade a straightforward interpretation concerning the key drivers behind the landscape mosaic. Our research shows that the high-level drivers of the land cover - land use mosaics, characteristic of the basaltic tablelands of northern Rio Grande do Sul, Brazil, can be identified based on analysis of the vegetation pattern in relation to geomorphic and pedogenetic phenomena controlling water and nutrient supply, together with human action. The analysis is implemented on two spatial scales: one regional, embracing a large portion of tablelands, and the other at the landscape scale by selecting three contrasting sites. Natural grasslands (*campos*) still extend over much of the highest plateaus, on young but nutrient-depleted inceptisols. While on the lower altitudes campos over deep oxisols have been extensively replaced by cash crops. The *Araucaria angustifolia* montane forest characterizes the higher tablelands, where it occurs in habitats with a permanent water supply and out of the reach of the frequent grasslands fires. Semideciduous forests occur on the lower plateaus, restricted to the wet conditions of the bottomlands. In any case, the increasingly widespread human disturbance renders the natural pattern fuzzy, but the close correspondence between more fertile habitats and forest occurrence suggests that nutrient availability plays a key role. Nutrient availability, in turn, results from enhanced rates of erosion wearing out the ancient peniplain and further developing the drainage system. A conceptual model relating geomorphic, pedogenetic and human factors is proposed to explain the original and actual vegetation mosaics.

Key words: *Araucaria angustifolia* forests, landscape dynamics, subtropical grasslands, subtropical semideciduous forests, Vegetation mosaics

RESUMEN

Los paisajes que muestran mosaicos de ecosistemas naturales contrastantes, como bosques y pastizales, frecuentemente resultan de difícil interpretación en cuanto a los factores operativos detrás de dichos mosaicos. Nuestro trabajo en los altiplanos efusivos de Rio Grande do Sul, Brasil, muestra que los factores responsables de los mosaicos de cobertura-uso de la tierra a escala regional, pueden identificarse analizando los patrones de vegetación y su relación con procesos geomorfológicos y pedológicos que controlan la oferta de agua y de nutrientes, a los que se superponen procesos ligados al uso de la tierra. El análisis se llevó a cabo en dos escalas espaciales, la regional que abarcó una porción significativa de los altiplanos, y la local (del paisaje) en tres sitios contrastantes por sus características físicas y de uso. Los pastizales naturales o campos aún cubren buena parte de las mesetas más altas sobre suelos jóvenes (inceptisoles) pero muy empobrecidos en nutrientes, en tanto que en las mesetas a menor altitud, los campos (sobre oxisoles profundos), han sido extensivamente remplazados por cultivos anuales. Los bosques montanos dominados por *Araucaria angustifolia* se encuentran en las mesetas altas, restringidos mayormente a sitios con provisión de agua todo el año y fuera del alcance de los incendios del pastizal. El bosque semidecíduo se limita a las mesetas bajas donde ocupa las posiciones topográficas más bajas. En todos los casos el uso actual, agrícola o forestal, dificulta la interpretación, pero la estrecha correspondencia entre sitios con mayor disponibilidad de nutrientes y bosques sugiere que el factor nutricional desempeña un rol esencial en los actuales patrones de vegetación. A su vez la disponibilidad de nutrientes o fertilidad potencial está condicionada por la erosión de la peniplanicie y el rejuvenecimiento del paisaje producido por la erosión regresiva de los cursos de agua. Presentamos finalmente un modelo conceptual de la distribución de los ecosistemas naturales y del uso de la tierra, donde se interrelacionan todos estos procesos operativos a distintas escalas espaciales y temporales.

Palabras clave: bosques de *Araucaria angustifolia*, bosques semideciduos subtropicales, dinámica del paisaje, Mosaicos de vegetación, pastizales subtropicales, bosques semideciduos subtropicales, dinámica del paisaje

INTRODUCTION

Natural mosaics of forests and grasslands occur in many continental areas under different climates, environmental conditions and variable disturbance pressures. Such mosaic landscapes have been reported in South Africa (Ellery *et al*. 1992), Southwest United States (Huebner and Vankat 2003), central Australia and Tasmania (Bowman *et al.* 2004, 2007). The controlling factors, or 'drivers' in short, behind the mosaic can be in the specific climate and soil conditions, vegetation history, human interference, or in any combinations. The patchiness itself is a very puzzling matter considering that the mosaic is a sign of enhanced ecosystem turn-over in space and almost certainly far-from-equilibrium conditions. The relative contribution of different environmental drivers to controls in the mosaic determines the stability of the spatial configuration of the vegetation. As such, disturbance processes tend to produce more transient arrangements while physical-environmental factors tend to produce more conservative effects. Yet, to weigh the importance of each environmental driver is always a matter of active debate, highly dependent on the spatial and temporal scale at which the mosaics are interpreted.

Other forest-grassland mosaics, occurring in transitional areas between biomes dominated by either physiognomy (Huebner and Vankat 2003, Simonson and Johnson 2005), have drought and fire as the two key factors controlling the presence of grasslands and inhibiting the advance of forest. Under wet climates, where extensive drought periods seldom occur, few cases have been analyzed, mostly within the tropics. The extensive tropical savannas intermingled with semideciduous and evergreen forests (see Furley *et al*. 1992) and the high-altitude Andean grasslands (páramos) mixed with Polylepis dominated forests (Monasterio 1980) are two well known examples. Although the limit between grasslands and forests at high altitudes clearly correlates with mean ground temperatures (Koerner and Paulsen 2004), in the case of the analogous ecosystems at the tropical lowlands the natural factors that drive separation are water availability and nutrient status (Sarmiento and Pinillos 2001). In both cases, other factors shape the critical threshold of the leading drivers and scale the phenomenon in time and space.

Many aspects of the ecological puzzle concerning the dynamics of forest-grassland mosaics in the humid subtropics are still awaiting attention. It is quite clear from the literature, that a most neglected aspect of the puzzle is the effect of terrain and soil evolution. Likewise, the large extent to which these areas have been transformed by humans makes necessary a deeper understanding of the effect of environmental drivers on the spatial location of dominant land-use patterns. These both should deserve further study in order to understand the current natural and non-natural mosaic patterns. To the main utility in these, besides their scientific value, is the laying of foundations for reliable forecast of change.

In this paper we aim to establish the identity of causal mechanisms linking the spatial pattern of the vegetation to the spatial patterns of high-level environmental drivers in the basaltic tablelands of Southern Brazil. Specifically, our paper clarifies the functionality and dynamics of local landscapes in terms of terrain and soil evolution, natural ecosystems distribution and land use change. We pay particular attention to the effect of spatial scale to fix the conditions in the ecological realm within which the proposed mechanisms apply.

METHODOS

Study area

We selected a region bounded by 27º to 30ºS and 55º to 49º 30' W within the northern half of Rio Grande do Sul, in southern Brazil (Fig.1). Within this area we restricted our analysis to the extensive basaltic tablelands where natural grasslands and forests intermingle. The current relief of the tablelands is an almost level peniplain, formed during the Tertiary and the Quaternary by several successive peniplanation processes. These gave the land a gently undulating surface, the peniplain, denuded by erosion (BRASIL 1986). A coarse-grained landscape emerged, with fairly flat tops and scatter mammillary hills, divided into fragments by a rectangular drainage system strictly controlled by a dense system of crossing faults. The current surface abounds of rocky ridges, gentle sided hills, and abrupt scarps, some reaching up to one hundred meters height towards the plateau's eastern edge. The lava plateau reaches its highest elevation where it meets the coastal plain with its spectacular vertical cliffs more than 1000 m high. The plateau's altitude decreases to 200 m *asl.* at its western boundary formed by the Uruguay River. Although cash crop agriculture and forestry covers a large part of the region, the recurrent motif of the herbaceous matrix, interspersed by forest groves and gallery forest networks, confer a homogeneous character to the entire tableland (BRASIL 1986, Pillar and Quadros 1997, Pillar 2003; Oliveira and Pillar 2004).

In spite of temperature differences driven by altitude over the entire study area, a subtropical humid climate prevails under which neither the water regime nor temperature constrain the development of the forest. This being so, the original forest-grassland mosaic have been thought of as the result of the Quaternary history of climate change and human influence. The relevant hypothesis states that grasslands are relict formations of the last glacial age in the process of being replaced by forests. But, as the hypothesis continues, human-driven disturbances, mainly fire and grazing have prevented a complete replacement (Behling 2002, Behling *et al*. 2004, 2005, Pillar 2003, Dümig *et al.* 2008).

Despite the persistence of the paleo-ecological footprints and an increasingly widespread human disturbance, there is also a striking correspondence between spatial patterns of forest-grassland mosaics and high-level drivers of the physical environment whose action may not be under the influence of the disturbance regime. These suggest that not all of the puzzling questions of coexistence and distribution patterns of contrasting ecosystems have yet been fully disentangled.

The forest area in Rio Grande do Sul, over 40% of which used to be covered by *Araucaria* forests,

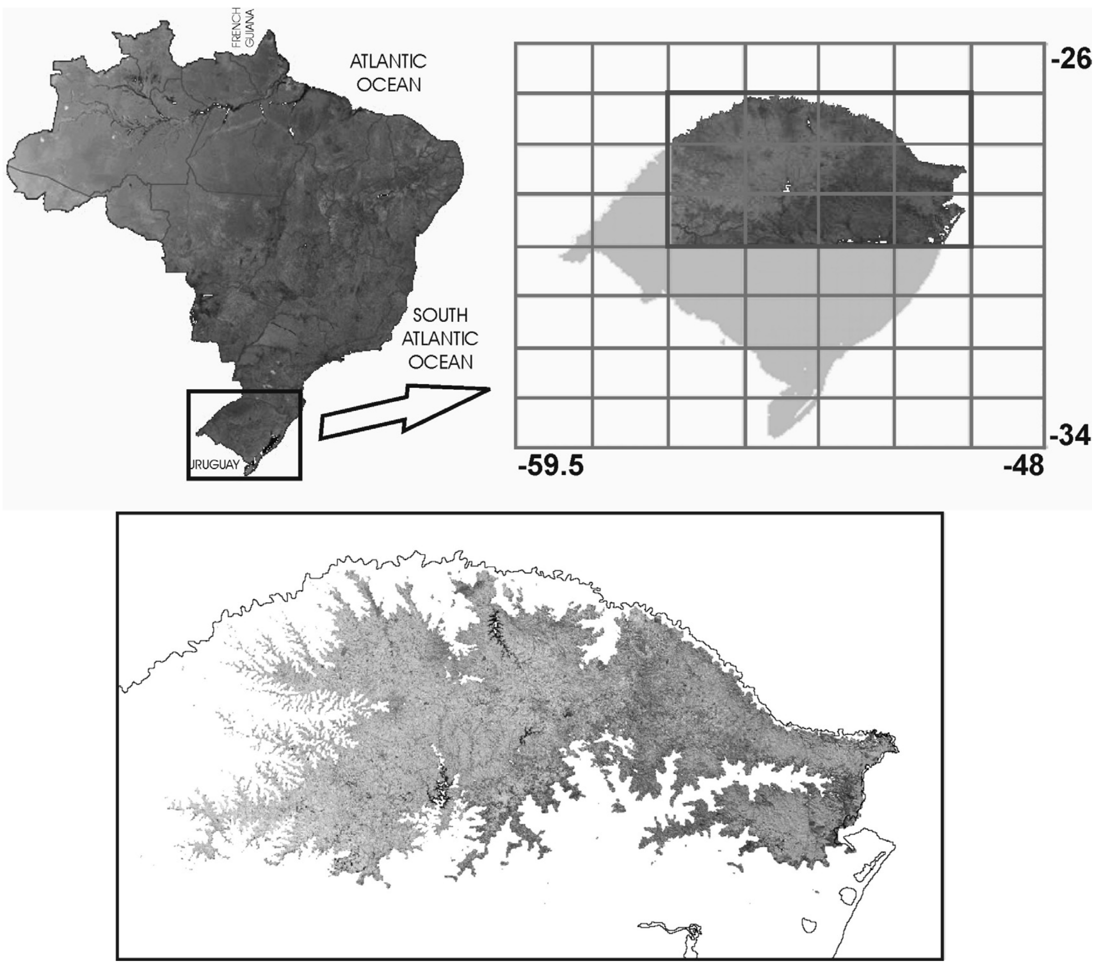

Figure 1. Location of the study area in Brazil and Rio Grande do Sul. Grid to the right gives geographical coordinates. Study area, enclosed by highlighted box, is bounded by 27º to 30ºS and 55º to 49º 30' W.

has plummeted to 3% today due to the concurrent pressure of logging, cattle raising and farming (Varty N. and Guadagnin D.L, 1996, Information sources on the biology, conservation and trade of species in Brazil. Unpublished document prepared for WCMC/SSC Conservation and Sustainable Management of Trees project). A similar fate has been dealt to the natural grasslands by afforestation and replacement of the native grasses by forage species. Today, forestry and agriculture play a dominant role in shaping the regional landscape. However, the constraints imposed by the environmental setting are as forceful drivers to control land-use spatial patterning as to set limits for the natural vegetation. As a result, the original distribution of natural vegetation can be traced almost everywhere.

River dissection and tectonics have partitioned the basaltic plateau into two large topographic units. The largest and lowest unit, known as '*Planalto das Missões*', extends over an altitudinal range from ca. 200 to 800 m *asl*. The dominant deep lateritic soils sustain a highly intensive agricultural system in which large farms, mechanization and the intense use of agrochemicals are all distinguishing features. Although the *Planalto das Missões* is largely uniform in terms of land use, soils and vegetation, in the '*Planalto das Araucárias*', the second topographic unit, two physiographic domains are easily identified. The first domain ranges from 800 to ca. 1000 m asl, mostly covered by lateritic soils of variable depth on which land-use has extensively led to the replacement of natural vegetation by cash crops (cereals - mainly wheat in winter and soybeans in summer, forages and pomes). The second domain is the highest and easternmost extension of the study area, comprising highlands ca. 1000 to 1200 m *asl*. Unlike the previous units, the dominant soil type is a shallow and highly dystrophic inceptisol (after the American Soil Taxonomy, *Cambissolo* in the Brazilian System of Soil Taxonomy). Agriculture here is marginal at best and forestry and cattle raising are the prevalent land uses.

Although natural vegetation is a mosaic of grasslands and forests over the entire basaltic plateau, noticeable floristic and functional differences set apart the natural ecosystems in the *Planalto das Missões* from the analogous higher up. The most striking difference is the share of deciduous and evergreen elements. The evergreen montane forest, dominated by *Araucaria angustifolia* (Bertol) Kuntze, is characteristic of the higher plateaus. At lower elevations prevails instead the semideciduous forest, with many tree species sharing the canopy such as *Ocotea acutifolia* (Nees.) Mez., *Nectandra lanceolata* Nees & Mart. ex Nees, *Cedrela fissilis* Vell., *Cabralea oblongifoliola* C. DC, *Cordia trichotoma* (Vell.) Arrab. ex Steudel and the palm *Syagrus romanzoffiana* (Cham.) Glassman. Interesting to note that while deciduous trees and palms are most frequent in the *Planalto das Missões*, evergreen species are dominant in the *Planalto das Araucárias*. Klein (1975) provides a succinct floristic description of the regional grasslands and forests. A detailed account of the distribution and characteristics of main landscapes in the study area can be found in FIBGE (1986, 1990).

Remoted-sensed imagery

Ortho-rectified, atmospherically corrected and shaded Landsat images (Bands 5, 4 and 3, from May to October 2001, geographical system SAD69) and the corresponding digital terrain model (EMBRAPA DTM, compatible cartographic scale 1:100,000, geographical system WGS84) provide remote-sensed data for our research. These were downloaded from the website of the Brazilian Agency for Agricultural Research (*Empresa Brasileira para a Pesquisa Agropecuária*, EMBRAPA, http://www.relevobr.cnpm.embrapa.br). EMBRAPA DTM is a ground-controlled terrain model based on the Shuttle Radar Topography Mission DEM. Technical information on the process of correcting, geo-referencing and assembling the Landsat bands and the DTM can be found in Miranda (2005). After re-projecting the Landsat bands into the WGS84 geographical system, we cross-controlled the Landsat bands and the DTM for positional differences. Projection changes on the Landsat bands were undertaken accordingly using a linear mapping function.

LCLU classification

Land cover / land-use (LCLU) classification was performed at the regional scale of the entire study area and at the local scale of three selected windows of ca. 225 km2, each window located in one of the physiographic landscape types previously identified. The first window (Santo Angelo) represents the *Planalto das*

Missões, the second (Vacaria) the physiographic domain of lesser altitudes in the Planalto das Araucárias, and the third (Cambará) the plateau's highest eastern portion. At the regional scale, we retrieved the Landsat bands resampled to a resolution compatible with the cartographic scale 1:250,000, but at the local scale the compatible cartographic scale of the bands was 1:25,000. In the two scales, LCLU was classified according to tone and texture, two context-dependent properties of pattern whose capture require some degree of generalization and spatial aggregation. Running windows of 7x7 pixels with 6x6 overlap were chosen to represent the neighborhood of any given central pixel. To assess a dominating tone, we submitted the bands to image generalization by Gaussian smoothing (Eastman 2006, Lee 1983), which outputs a weighted average of the running window, with average weighted more towards the value of the central pixels. Texture was estimated as the deviation around the mean of the running window. Thereafter, the six pattern-descriptors (two per band) were subjected to an iterative, self-organizing routine of classification, ISOCLUST (Eastman 2006). We ran the routine several times and produced as many maps as runs with different number of classes. Afterwards we selected the map predicting with greatest accuracy the land cover/land-use types recorded at 85 ground-proofing sites. We assigned to each class one of the following types: Campos, natural forests, wetlands, agriculture and forestry. Classes in which we could not determine a single prevailing LCLU were considered mosaics of their most common land-cover types.

LCLUs and terrain topography

We partitioned terrain topography into four concise descriptors: mean altitude, relative altitude, surface ruggedness and slope, each one indicative of land- and soil-forming processes of specific nature and spatial scale and so, also proven good indicators of the occurrence of the different soil types in the study area (see Streck 1992, Potter 1977, BRASIL 1986). Mean altitude defines the position of a pixel on the regional hypsithermal and potential energy gradients and in these terms is taken to be a product of tectonics. Relative altitude is taken to be the product of the local land-forming processes and in these terms describes pixel position in spatially-restricted catenae related to drainage and erosion. Surface ruggedness is indicative of regional rates at which soil stripping and dissection occur, and slope is a control of the intensity of local processes of soil erosion and aggradation. We derived mean altitude and surface ruggedness from the DTM as an altitudinal average and its standard deviation in running windows of 41 x 41 units, in which the reference pixel is at the reference windows centroid. Relative altitude was obtained by subtracting mean altitude from the actual altitude in the DTM and slope was calculated (in decimal degrees) as the angle of the maximum downhill slope considering the pixels to the top, bottom, left and right of the reference pixel (see Monmonier 1982).

Thereafter, we performed comparisons on the characteristic topographic traits of the LCLUs based on the the Newman-Keuls Q statistic. The Newman-Keuls test, also known as the *studentized* range test, is a pairwise comparison of means highly advised in situations in which (1) unequal group sizes may sensibly affect the significance of the mean differences, and (2) multiple comparisons may lead to the rejection of a true null hypothesis (see theory in Kendall & Stuart 1976, application in Orlóci 1995, Part II). At the regional scale, in these comparisons we set the pixel size roughly one square kilometer to be compatible with the cartographic scale of 1:1,000,000. Likewise, at the local scale, we used a pixel size roughly one hectare to be compatible with the cartographic scale of 1:100,000. We set the threshold probability of the test to a stringent 0.01.

Landscape analysis and interpretation

Focusing on the linkage between vegetation, soils and geomorphic processes, we looked for patterns that were either common to or specific of any of the two scales, as well as when compared the three sub-areas at the local scale. On that basis, we drew conclusions regarding the influence of the regional environmental setting on local landscape patterns and on the associated processes of spatial patterning. We integrated general aspects of topography, land forms and soil genesis within a frame of long-term geological events and frequent climate changes, in order to produce a conceptual model of landscape development with which to interpret LCLU composition and spatial arrangement at the two spatial scales under consideration. Special attention was given to the soils whose more salient features, such as depth, colour, layer structure and base saturation, were derived from the available literature: the general map of soils of Rio Grande do Sul at the 1: 750,000 cartographic scale (BRASIL 1973, Streck *et al*. 2002), and two soils surveys at the 1: 10,000 cartographic scale (Potter 1977, Streck 1992). Soil classes in Streck (1992) and Streck *et al*. (2002), presented after the Brazilian System of Soil Classification, were translated into the American Soil Taxonomy (AST) according to the guidelines provided by EMBRAPA (2006). The classes in Potter (1997), though already translated, had to be updated to the current version of the AST following Buol *et al.* (2003). The relation between topography and soils was extracted from the units' description in the reports. Regional patterns of association between LCLUs and soils were derived from the comparison of the LCLU map with the general map of soils (BRASIL 1973). Since both maps have different level of spatial generalization and differing sources of error, an uncertain proportion of the pixels is randomly allocated to each joint (LCLU – Soil) state. Therefore we based our discussion on the adjusted joint frequencies after error removal (residuals), assuming that error-due allocation of pixels follows a Chi-square distribution (Orlóci 1991). We interpreted the information altogether in terms of soil- and land-forming processes and then checked whether the spatial association of LCLU types, soils and topographic traits matched the expected on the basis of our conceptual model.

RESULTS

Regional scale

For the entire study area, the classificatory procedure applied to the Landsat bands identified three classes with unequivocal correspondence to single LCLU types. Two of them correspond to natural forests and grasslands and the third to croplands, including both cash crops and managed pastures. Two other classes corresponded to (i) mosaics of natural forests and tree plantations, and (ii) mosaics of forests and croplands (Fig. 2). Among the issues evident in the map, we point out the importance of croplands, which occupy

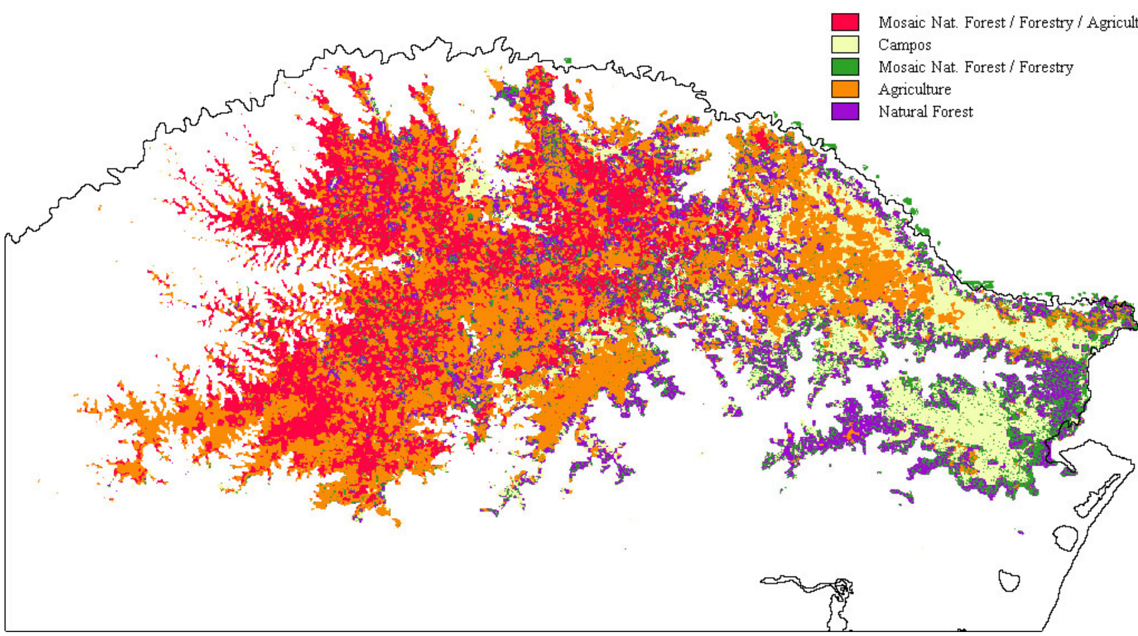

Figure 2. Land-cover, land-use (LCLU) classes in the basaltic tablelands of northern Rio Grande do Sul (27º to 30ºS and 55º to 49º 30' W). Classification from Landsat bands 5, 4 and 3, July 2001, resampled to a resolution compatible with the cartographic scale 1: 250,000. The corresponding RGB composite available at http://www.cdbrasil.cnpm.embrapa.br/rs/index.htm.

most of the lower plateaus and seem to advance very actively over the higher ones. Contrary to this, natural grasslands and semideciduous forests are very infrequent in the lower plateaus, generally occurring along creeks and other restricted environments. On the higher plateaus grasslands constitute the most extensive LCLU type, followed by Araucaria forests and pine plantations.

Average values and standard deviations for the topographic traits, in each regional LCLU type, appear in Table 1. Although standard deviations seem fairly large in comparison with the respective means, the Q-test reveals strikingly significant mean differences in almost all cases (Table 2). In general terms, mean altitude and ruggedness are the traits producing the largest differences among LCLU types. Slope and relative altitude produce the least and non-significant differences. These results come as no surprise given the spatial scale of the terrain-evolution processes associated with each trait. Regarding ruggedness, it is worth noticing that agricultural areas and mosaics of natural forests and agriculture clearly depart from the group of the remaining LCLU types, occupying the flattest portion of the plateaux. These LCLU types are also largely associated with the deepest and most evolved soils of the Ultisol (at the edge of the plateau) and Oxisol orders. On the contrary, the most broken terrain is characteristic of the forested LCLUs, which in turn are largely associated to young soil units of the Entisol, Inceptisol and Mollisol orders (Table 3).

Local scale

Within this overall picture, the maps obtained at the local scale show three somewhat contrasting landscapes (Figs.3, 4, and 5). In the first window (Santo Angelo), which extends over the lowest part of the tablelands at about 200 m altitude, two types of agro-ecosystems (croplands and tree plantations) cover almost half of the area. From the two original ecosystems, grasslands are the least frequent while natural forests, together with secondary shrublands cover about 44 % of the window. In the second sub-area (Vacaria), at altitudes around 1000 m *asl.*, croplands and orchards extend over 40 % of the landscape. Yet, natural grasslands and grassy wetlands still cover about one third of the total area, and montane forests about a quarter. In the third unit, Cambará, where the tablelands reach elevations of 1200 m *asl*. in the highest parts, grasslands including managed pastures and herbaceous wetlands occupy 62 % of the plateau, montane forest about 30 % and pine plantations a little less than 10 %. Notwithstanding these different patterns of LCLU's coverage, results at the local scale showed consistent trends of association between terrain characteristics and the LCLUs. In a gradient of relative altitude, forested areas occupied the ill-drained bottomlands, associated with the soils classified as *Fluvaquents* and *Argiaquolls*, while grasslands and croplands the higher positions on which old and deeper Oxisols (*Hapludox*) and Ultisols (*Paleumult* and *Paleudult*) dominate. Likewise, the highest values of ruggedness and slope distinguished forested lands as it also did at the regional scale. Table 4 summarizes LCLU coverage and topographic data in the three sub-areas.

Notwithstanding the fact that in the three cases LCLU types exhibit significant mean differences from one another in their topographic traits (Tables 5, 6 and 7), the Q-values reveal important differences among windows. In Cambará, as well as in Santo Angelo, higher differences are produced by mean altitude and relative altitude. In Vacaria instead LCLU types are more responsive to relative altitude and ruggedness.

Landscape analysis and interpretation

Cultural and natural landscapes

Either at the regional or at the local scale, cultural land gives its imprint to the whole landscape. To a large extent the current distribution of the different types of ecosystems is mostly due to farming, animal husbandry and forestry. Yet, the physical environment has played a forceful role shaping land-use dynamics. Croplands extension is evidently associated with elevation on the plateaus and almost disappears above 1000 m *asl*. Elevation, in turn, influences minimum temperatures and frost frequency. In the low tablelands where Santo Angelo is located, a warm subtropical climate prevail with less than 15 frost days and absolute minima from -4º to -7 ºC. In the *Planalto das Araucárias*, up to 1000 m *asl*., fairly severe winters with up to 20 frost days occur and the absolute minima approaches -8ºC. Further upwards frost incidence is the greatest, with up to 30 frost nights and just one frost-free season

Table 1. LCLU types at the regional scale described in terms of topographic traits and coverage. SD: Standard Deviation. AGR, agriculture. NF / AGR, mosaic of natural forests and croplands. NF / FTY, mosaics of natural forests and forest plantations. NF, natural forests. GLD, grasslands.

			LCLU Classes				
			AGR	NF / FTY / AGR	NF / FTY	NF	GLD
Topographic traits	Mean Altitude	Mean	559.65	474.80	736.38	690.06	790.33
		SD	188.34	112.07	216.28	189.83	196.67
	Relative altitude	Mean	1.73	2.85	2.36	1.92	1.89
		SD	19.88	17.03	30.86	30.66	23.04
	Ruggedness	Mean	23.36	20.75	36.73	36.03	28.36
		SD	9.63	5.92	17.88	16.05	10.57
	Slope	Mean	4.23	3.82	6.27	6.42	5.05
		SD	2.91	2.11	4.66	4.61	3.51
	Coverage	Pixels ≈ Km^2	11121	7146	3302	4530	4583
		%	36.25	23.29	10.76	14.76	14.94

Table 2. Standardized mean differences (Q-values) from the topographic traits in Table 1, among regional-scale LCLU types. In *italics*, larger and smaller Q-values per trait. In **bold**, non significant Q-values. Significance is given to any absolute Q-value higher than $Q_{(\alpha=0.01,\ p=2,\ df>1000)} = 3.64$. α = error probability threshold. p = Number of contrasted LCLUs. df = degrees of freedom.

Mean Altitude	Agriculture	Nat. Forest / Forestry / Agriculture	Nat. Forest / Forestry	Natural forest
Nat.Forest /Agriculture	-44.30			
Nat.Forest / Forestry	70.59	98.41		
Natural Forest	58.57	89.73	*-16.02*	
Grasslands	104.03	*131.99*	18.71	37.89
Relative Altitude	AGR	NF / FTY / AGR	NF / FTY	NF
Nat.Forest /Agriculture	*4.53*			
Nat.Forest / Forestry	**1.95**	**-1.43**		
Natural Forest	**0.66**	**-3.00**	**-1.18**	
Grasslands	**0.56**	**-3.11**	**-1.26**	***-0.09***
Ruggedness	AGR	NF / FTY / AGR	NF / FTY	NF
Nat.Forest /Agriculture	-21.28			
Nat.Forest / Forestry	83.38	93.86		
Natural Forest	88.85	*99.44*	*-3.78*	
Grasslands	35.21	49.70	-45.32	-45.25
Slope	AGR	NF / FTY / AGR	NF / FTY	NF
Nat.Forest /Agriculture	-11.31			
Nat.Forest / Forestry	43.07	48.71		
Natural Forest	51.98	*57.28*	***2.74***	
Grasslands	19.55	27.19	-22.36	-27.36

Table 3. Adjusted joint frequencies of the regional LCLU classification in Map 2 and the soil units in the General Map of Soils of Rio Grande do Sul (BRASIL 1973, Streck et al. 2002). Positive values (**in bold**) result from a joint state larger than the expected error (positive spatial association between the LCLU type and the soil class). Frequencies below the expected error are negative. LCLU legends as in Table 1, soil legends provided after the nomenclature of the General Map of Soils: **CHa1**: Low base-saturation and Al+++ enriched Inceptisols, with organic-matter enriched topsoil. **CLa**: Low base-saturation and Al+++ enriched Inceptisols, with histic horizon on top. **LBa** : Oxisols with dark, organic-matter enriched topsoil. **LVaf** : Red, Fe Al sesquioxides enriched Oxisols. **LVaf** / **RLe**: Mosaic of red Oxisols and shallow, eutrophic Entisols. **LVd – LVdf**: Red Oxisol. **MTf / RLe**: Mosaic of Mollisols with argillic horizon and shallow, eutrophic Entisols. **NVdf**: Red Alfisols and Ultisols with dystrophic and Fe+++ enriched horizon. **PVAa – PVAf**: Yellow-red Ultisols. **PVAa - PVd / RL**: Mosaic of yellow-red and red Ultisols with lithic Entisols. **PVd**: Red Ultisols. **RLd / CH**: Mosaic of dystrophic Entisols and dystrophic Inceptisols. **RLd**: Dystrophic and shallow Entisols. **RLe**: Eutrophic and shallow Entisols and Mollisols. **RLe / VE**: Mosaic of eutrophic Entisols and Vertisols.

	AGR	NF / FTY / AGR	NF / FTY	NF	GLD
CHa	-13606.39	-10232.52	**7032.89**	**2266.80**	**14539.22**
CLa	-784.87	-1044.24	**1052.27**	**448.10**	**328.73**
LBa	-1669.14	-7517.40	**463.14**	-418.94	**9142.34**
LVaf	**8623.43**	-3515.78	-2458.03	-365.39	-2284.23
LVaf / RLe	-103.52	**121.87**	-38.18	-87.03	**106.87**
LVd - LVdf	**3790.96**	**30866.21**	-7311.03	-10330.30	-17015.83
MTf / RLe	-3157.27	-5169.51	**2214.89**	**5771.40**	**340.50**
NVdf	-498.18	**1549.92**	-427.72	**491.24**	-1115.27
PVA(a+d)	**1307.06**	**955.18**	-892.85	-128.67	-1240.72
PVAa - PVd / RL	**5974.15**	-3255.60	-909.03	-1373.03	-436.48
PVd	-41.24	-26.52	**47.35**	**32.21**	-11.80
RLd / CH	-4719.99	-3336.66	**2103.46**	**5214.68**	**738.52**
RLd	**4815.49**	-895.52	-341.74	-1508.19	-2070.04
RLe	-27.34	**989.16**	-378.57	**202.78**	-786.02
RLe / VE	**96.85**	**511.43**	-156.82	-215.66	-235.80

(summer). Absolute minima are as low as – 8º to -10ºC and snowfall is not uncommon (see Nimer 1977). However, frost does not seem to be the sole constrain given that even in the highest regions frost nights would spare summer crops. Undoubtedly, soil features must also play a key role.

Deep Oxisols on top of the old peniplain present a characteristic gentle surface and are the most frequent soil types in Santo Angelo and Vacaria. Both ruggedness and relative altitude connect the widespread occurrence of croplands there with this type of soils, whose depth and texture make them prone to mechanization and enhance soil water retention. On the contrary, in Cambará the dominant Inceptisols are in general shallow soils. Commercial tree plantations, *Eucalyptus* species in the lower tablelands, *Eucalyptus* and *Pinus* at intermediate sites, and *Pinus* at higher elevations, occupy increasingly important areas in the three landscapes. On the deep soils of Santo Angelo and Vacaria, tree plantations are not as extensive as croplands, being mostly restricted to the lower hill slopes where shallower soils occur. The forestry lots are rather small, just a few hectares, whereas in the eastern plateau, pine plantations have increasingly taken over the entire area, with lots that may cover hundred of hectares. Montane Araucaria forests are quite extensive in the high

Table 4. LCLU types classified at the local scale in three sub-areas within the broad study area. Types are described in terms of topographic traits and coverage. SD: Standard Deviation.

LFT	CLASS	MEAN ALTITUDE		RELATIVE ALTITUDE		RUGGED-NESS		SLOPE		N	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Pixels ≈ has	%
CAMBARA	Natural Forests	979	38.35	-6.22	26.62	30.72	7.03	6.46	4.13	4642	29.71
	Forestry	1004	37.39	2.15	26.26	31.18	5.92	5.80	4.02	1307	8.36
	Grasslands	970	33.84	3.34	20.92	28.08	6.45	4.70	3.20	9677	61.93
STO ANGELO	Forests and Shrublands	337	34.03	-2.84	15.54	19.87	3.08	3.60	1.93	6854	43.87
	Forestry	328	33.84	-7.94	16.11	19.70	2.98	3.48	2.08	2050	13.12
	Grasslands	340	33.77	2.85	14.99	19.49	3.16	3.52	1.77	2009	12.86
	Agriculture	346	35.97	7.55	12.24	19.01	2.85	2.96	1.40	4712	30.16
VACARIA	Natural Forests	920	16.60	-2.27	9.43	12.44	6.46	2.45	1.68	3944	25.41
	Wetlands	919	16.61	-2.30	7.48	10.33	4.22	2.09	1.26	2714	17.48
	Grasslands	921	15.90	0.74	7.20	10.07	3.72	2.11	1.17	2640	17.01
	Agriculture	922	17.78	2.09	7.40	10.49	4.24	2.07	1.25	6225	40.10

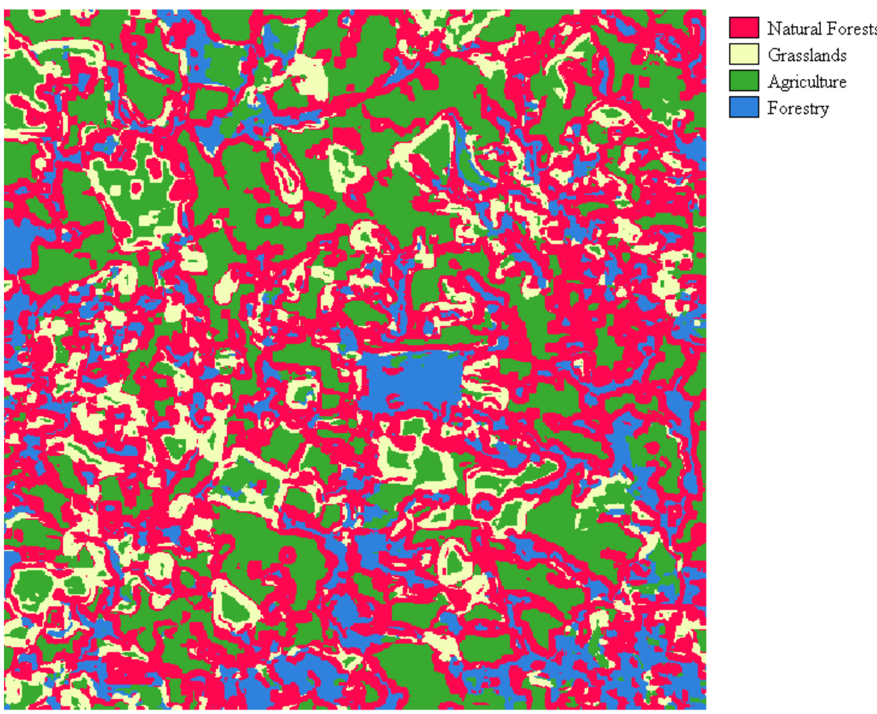

Figure 3. LCLU classification, local scale, Santo Angelo area. Image central point at: 28o11’15”S / 54o11’15”W, 500 x 500 pixels, proximate pixel size 30 m. RGB composite (Landsat bands 5, 4 and 3) available at http://www.cdbrasil.cnpm.embrapa.br/rs/htm0/rs17_46.htm

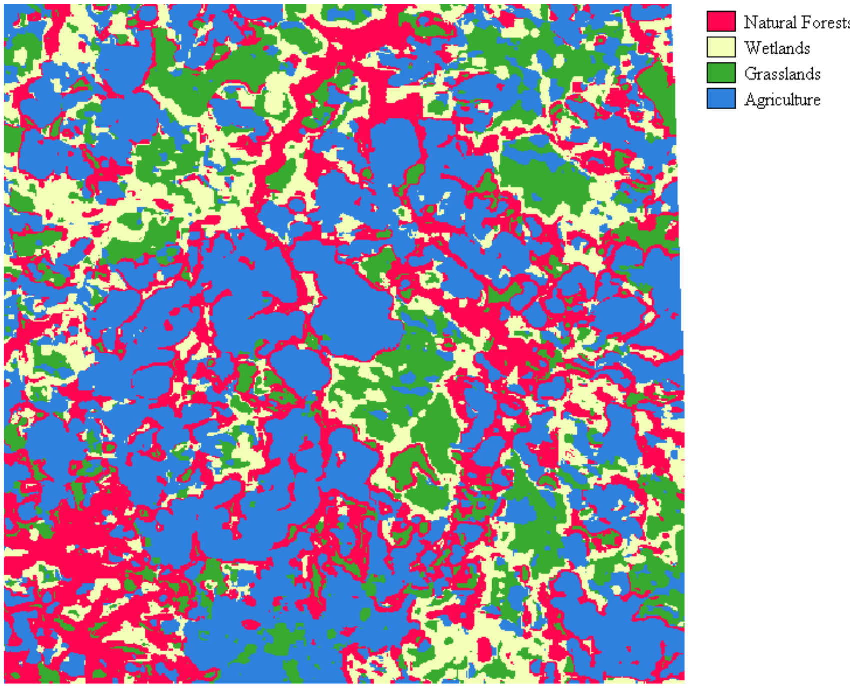

Figure 4. LCLU classification, local scale, Vacaria area. Image central point at: 28o26'15"S / 50o56'15"W, 500 x 500 pixels, proximate pixel size 30 m. RGB composite (Landsat bands 5, 4 and 3) available at http://www.cdbrasil.cnpm.embrapa.br/rs/htm0/rs19_72.htm

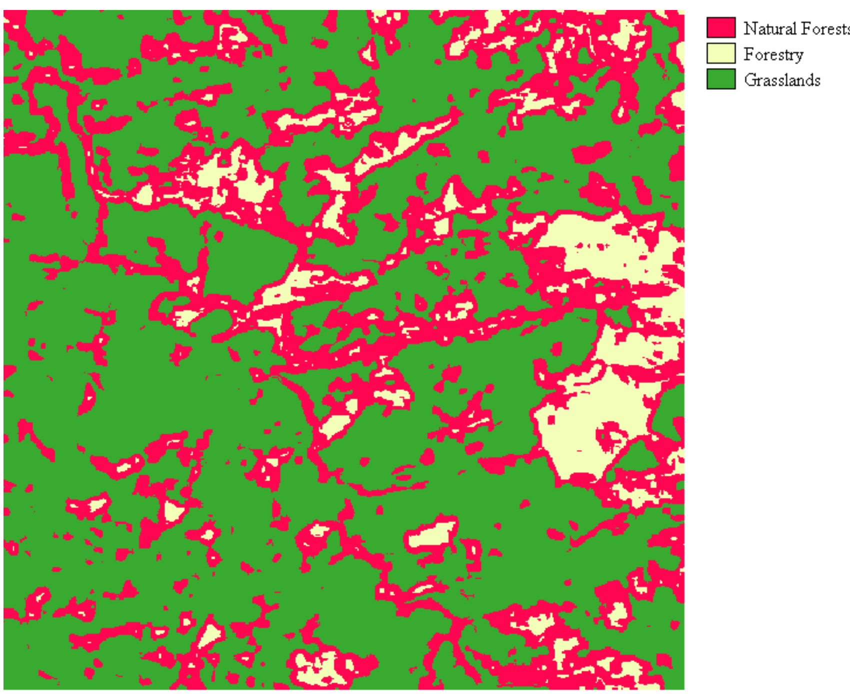

Figure 5. LCLU classification, local scale, Cambará-Bom Jesus area. Image central point at: 29o03'45"S / 50o11'15"W, 500 x 500 pixels, proximate pixel size 30 m. RGB composite (Landsat bands 5, 4 and 3) available at http://www.cdbrasil.cnpm.embrapa.br/rs/htm0/rs24_78.htm

tablelands. Natural grasslands, still conspicuous in Vacaria and widespread in Cambará, have been almost totally eliminated in Santo Angelo.

The linkage between land forms, soils, vegetation and land use

In the lowest tablelands of the Santo Angelo area deep oxisols (*Hapludox*) overtopping a quite thick weathering mantle extend across the upper topographic positions, formerly occupied by grasslands and now dominated by croplands. Shallow soils like dystrophic inceptisols evolving under humid conditions (*Dystrudepts*) and eutrophic mollisols, with argillic horizons evolving under per-humid regimes (*Argiaquolls*), cover the most deeply eroded slopes: inceptisols over denuded basalt and mollisols on colluvial deposits (Streck 1992). While mollisols have a negligible relative extension and can hardly be noticed in Landsat images, *Dystrudepts* form an intermediate fringe between the *Oxisols* and the bottomland soils. By the beginning of the 1990s these were mainly covered by semideciduous forests (Streck 1992), but by the time of the Landsat image (winter season of 2001) most of their area had been taken by croplands. Young humic gleys (*Fluvaquents*) characterize the network of ill-drained bottomlands, more extensive here than in the Vacaria landscape and much more extensive than in Cambará.

We classified the window of Santo Angelo into four LCLU classes (Fig. 3), which differ from one another in their topographic traits (Tables 4 and 5). Crops occupy the highest relative altitudes, where slope and ruggedness are the lowest (characteristics of the latossolic areas), while the scattered grasslands occur in intermediate positions, forming isolated fringes around the agricultural fields. Semideciduous forests dominate in the lowest positions together with herbaceous wetlands on ill-drained soils, where ruggedness and slope are highest (characteristic of young soils). Under similar conditions, patches of tree plantations and shrublands occur, suggesting the expansion of plantations over the semideciduous forest and the connection of shrublands to secondary communities after clearing.

A different pattern is found over the almost flat plateau in Vacaria, 350 km eastwards. There, oxisols evolving under a per-humid regime

Table 5. Pairwise comparisons in terms of standardized mean differences (Q-values) from topographic traits in Table 3, among the local-scale LCLU types at Santo Angelo. *In italics*, larger and smaller Q-values per trait. **In bold**, non significant differences. Significance rule in table 2.

Mean Altitude	Nat. Forests /shrublands	Forestry	Grasslands
Forestry	-14.63		
Grasslands	*4.84*	15.64	
Agriculture	19.46	*27.83*	9.21
Relative Altitude	N.Forest / Shr	Forestry	Grasslands
Forestry	-14.63		
Grasslands	*4.84*	15.64	
Agriculture	19.46	*27.83*	9.21
Ruggedness	N.Forest / Shr	Forestry	Grasslands
Forestry	**-3.17**		
Grasslands	-7.03	***-3.14***	
Agriculture	*-21.34*	-12.24	-8.46
Slope	N.Forest / Shr	Forestry	Grasslands
Forestry	-3.77		
Grasslands	**-2.49**	***1.01***	
Agriculture	*-26.75*	-15.55	-16.63

(*Hapludox*) and covering about half of the area, overtop a rather thin weathering mantle (Potter 1977). Entisols are developing on isolated rocky crests and ridges, where erosion has washed out both the regolith and the former soil; they barely attain five percent of the area merging in the image with the surrounding soils to appear uniformly covered by grasslands (Fig. 4). Our field data suggest that these lithic entisols are associated with shrubby grasslands and eventually with small groves. On steeper middle and lower slopes, mostly covered by colluvia, rather old acidic ultisols (*Palehumults* and *Paleudults*) occur. They exhibit organic-matter-enriched topsoils and a slight (if any) clay concentration gradient throughout the profile. A forest-dominated mosaic of montane forests and grasslands extended over these ultisols by the end of the 1970s (Potter 1977), but in the Landsat image annual crops had already replaced the original vegetation. Moderately young inceptisols (*Humaquepts*), evolving under per-humid to moist regimes, extend over the seasonally waterlogged bottomlands, show humic topsoils and mostly maintain montane forests and grassy marshes.

Ruggedness (closely mirrored by slope) and relative altitude are the main differences among LCLU types (Tables 4 and 6). Sharply distinct are riparian forests, located at the lowest positions of the toposequences, where ruggedness and slope are the largest. Although forests and wetlands do not differ significantly in terms of relative altitude, which means that these LCLUs occur together in the bottomlands, they do largely differ in terms of ruggedness and slope. The gentler topographies characterizing the wetlands indicate a poor development of the drainage network. Both observations suggest the association of forests with young soils on areas of intense drainage incision. Conversely, grasslands and croplands exhibit fairly similar topographic traits, suggesting that agriculture has mostly expanded over natural grasslands. There is also a mixed unit of forests and shrublands, whose location in terms of relative altitude is similar to that of grasslands and agricultural fields, though it marks more irregular topographies. This unit seem to correspond to the *Palehumults* domain and, given its spatial association with the agricultural lands, shrublands seem to be associated with land

Figure 6. Pairwise comparisons in terms of standardized mean differences (Q-values) from topographic traits in Table 3, among the local-scale LCLU types at Vacaria. *In italics*, larger and smaller Q-values per trait. **In bold,** non significant differences. Significance rule in table 2.

Mean Altitude	Nat. Forest	Wetlands	Grasslands
Wetlands	**-3.34**		
Grasslands	***3.31***	6.10	
Agriculture	8.19	*10.87*	**3.59**
Relative Altitude	Nat. Forest	Wetlands	Grasslands
Wetlands	***-0.21***		
Grasslands	21.30	19.79	
Agriculture	*38.12*	33.96	10.34
Ruggedness	Nat. Forest	Wetlands	Grasslands
Wetlands	-24.80		
Grasslands	-27.62	**-2.79**	
Agriculture	*-28.08*	***2.04***	5.30
Slope	Nat. Forest	Wetlands	Grasslands
Wetlands	-14.99		
Grasslands	-14.04	***0.76***	
Agriculture	*-19.38*	**-0.90**	**-1.79**

fallow rather than to a natural process of forest expansion over grasslands.

The LCLU classes in Cambará greatly differ in terms of all the topographic descriptors under consideration (Table 7), giving a consistent pattern in which natural forests occur on the lowest positions of local catenae and grasslands and managed pastures occupy the highest positions instead, along with forest plantations. Once again, the grasslands have distinctively low values of ruggedness and slope that set them apart from the forested LCLUs. Although there are not important differences between natural forests and forest plantations in terms of slope or ruggedness, the extension of commercial forests notoriously increases with mean altitude. This trend, which is consistent with the distribution of natural forests and mosaics of natural forests / forestry along the regional altitudinal gradient (Table 1), is the apparent response to the proximity of sawmills and their associated settlements, which are located to the east of the plateau.

Several classes of *Hapludox* have been recognized in Vacaria and Santo Angelo, according to their soil water regime and position in gradients of relative altitude (Potter 1977, Streck 1992). Yet, in soil catenas throughout the oxisol-dominated area, these highly weathered soils always occupy the rather flat top of the tablelands and the upper slopes, exception made of the residual rocky hills and crests which are topped with lithic entisols. Physical and chemical characteristics of the oxisols surely are important vegetation drivers. Firstly, their depth, good drainage conditions and clay texture assure large water storage at field capacity, preventing either a pronounced water deficit period during the drier years or water saturation during the rainiest season. In the second place, they are highly dystrophic as may be inferred from the very low figures of exchangeable bases, their negligible available P, and high Al^{3+} saturation (Table 8). The almost complete lack of primary minerals in the profile and the usually several-meters-deep weathering front, complete the scenario of nutrient constraint. In contrast, entisols are quite shallow, about 20 to 50 cm, and occur in fact in the driest habitats, though their stony nature promotes infiltration and fissures in the outcropping rock may serve as water reservoirs. Entisols may be either eutrophic or dystrophic, depending on their declivity and consequent lixiviation rates. When they occupy sediment-filled valleys, where rainwater seepage, an organic carbon-enriched A_1 horizon exist (characteristic of the *Fluvaquents*), being then either covered by gallery forests or by grassy wetlands. It is to be noticed that as the drainage system develops, forest frequency in the bottomlands increase. Other soil orders (ultisols, alfisols, mollisols and inceptisols) predominate on the relatively steeper hill slopes and over the bottomlands.

Table 7. Standardized mean differences (Q-values) among the local-scale LCLU types at Cambará. *In italics*, larger and smaller Q-values per trait. **In bold,** non significant differences. Significance rule in table 2.

Mean Altitude	Nat. Forest	Forestry
Forestry	31.77	
Grasslands	*-20.06*	*-45.91*
Relative Altitude	Nat. Forest	Forestry
Forestry	16.28	
Grasslands	*32.61*	***2.46***
Ruggedness	Nat. Forest	Forestry
Forestry	***3.15***	
Grasslands	*-31.74*	-22.58
Slope	Nat. Forest	Forestry
Forestry	-8.34	
Grasslands	*-39.02*	-14.78

Oxisols do not occur at all towards the eastern part of the plateau, above an altitude of ca. 1,000 m *asl*. Dystrophic inceptisols (*Dystrudepts*) become instead the most extended soil unit. In spite of their young age, these soils developed over acid volcanic rocks (rhyodacites and rhyolites), most often on hill slopes with a thin cover of colluvial material, are more dystrophic than the oxisols of the lower tablelands, as may be inferred from their very low exchangeable bases (Table 8). However, the A_1 horizon has the highest organic matter content of any other soil in the whole area, probably due to a long and uninterrupted evolution under grasslands. The apparent paradox between young age and high desaturation may be understood when considering that the colluvial material in which they are evolving has been thoroughly weathered in previous soil-forming cycles, being already depleted of primary minerals before its accumulation over the hill slopes. Thence, *Dystrudepts* develop from inherited kaolinitic clays, Fe and Al sesquioxides. In some places dystrophic inceptisols do not occur over colluvial deposits but seem to be evolving over eroded paleosoils, whose A horizon has been washed away, forming a new A_1 within the former, highly developed and weathered B horizon.

Despite the prevalence of highly dystrophic, polycyclic soils all over the three landscapes, they sharply differ from each other in terms of frequency of the different soil orders: in fact oxisols are much more extended in Santo Angelo than in Vacaria (notwithstanding their similar parent material), while very acidic ultisols (*Palehumults*) and inceptisols (*Dystrudepts*) are only conspicuous in the higher Cambará tablelands. These differences point out to significantly different environmental conditions controlling soil and landscape evolution throughout the last millennia.

On a conceptual model of vegetation dynamics and landscape development

Our analysis focuses on the key environmental and human-related aspects that more likely control patterns of spatial association between LCLUs, land forms and soils over the tablelands of northern Rio Grande do Sul. The broad conceptual framework includes the geological, climatic and geomorphic settings to which land- and soil-forming processes respond, together with the consequences of fire and land use. In the three examined landscapes, grasslands tend to occupy the nutrient depleted, acidic soils covering most of the relict peniplains whose characteristic soils are either deep oxisols (up to ca. 1000 m *asl*) or shallow inceptisols, while forest vegetation increasingly predominates on areas whose soil profile have been rejuvenated either by surface stripping, dissection or aggradation. It remains uncertain whether this fact has anything to do with primary minerals or nutrient availability in

Table 8. Some characteristics of soil profiles in the three areas analyzed at the local scale. The two figures for some features correspond to the A_1 and B_2 horizons. [1] Profile number in BRASIL 1986 (Cambará / Bom Jesus and Vacaria) and Streck 1992 (Santo Angelo). [2] This soil in a field crop has been limed, fertilized and plowed. [3] In the B_2 or the (B) soil horizon. CEC: Cation exchange capacity, S: Sum of exchangeable bases, V: Bases saturation, Al+++: Exchangeable aluminium, P assimil: Assimilable phosphorus.

Area	Cambará / Bom Jesus		Vacaria			Santo Angelo	
Profile Nr[1]	22	20	19	18	16	3	8
USSS soil unit	Haplumbrept	Palehumult	Haplhumox	Umbrorthox	Paleudult[2]	Haplorthox	Hapludalf
Depth (cm)	68 / +180	30 / 320	55 / 190+	34 / 330+	10 / 320	60 / 198+	16 / 83
CEC meq/100g clay[3]	24	15	13	15	18	9	16
S meq/100g soil	2.7 / 0.4	3.1 / 0.7	5.6 / 0.8	3.5 / 0.8	8.1 / 5.2	2.2 / 0.7	10/07
V %	09/03	19/06	23/08	16/05	53 / 17	20/08	56 / 45
Al+++ %	23 / 51	22 / 39	01/11	20 / 44	01/01	50 / 80	02/10
P assimil. (ppm)	03/01	< 1 / < 1	02/01	02/01	04/01	04/04	07/04

the soil profile, but it surely appear as a fruitful working hypothesis. Our conceptual model of forest – grassland occurrence (Fig. 6) and the location of the different LCLUs, applies to the three landscapes identified at the local scale and fits acceptably well the overall patterns observed at the regional scale.

Given the small to moderate development of the drainage system on the tablelands, forest expansion throughout the last millennia seems to have been concomitant with the progressive formation of the net of stream channels. There is, however, a situation in which the balance toward forests or grasslands is not clear, which is the domain of some ancient ultisols where the mosaics display the most dynamic ecosystem turnover

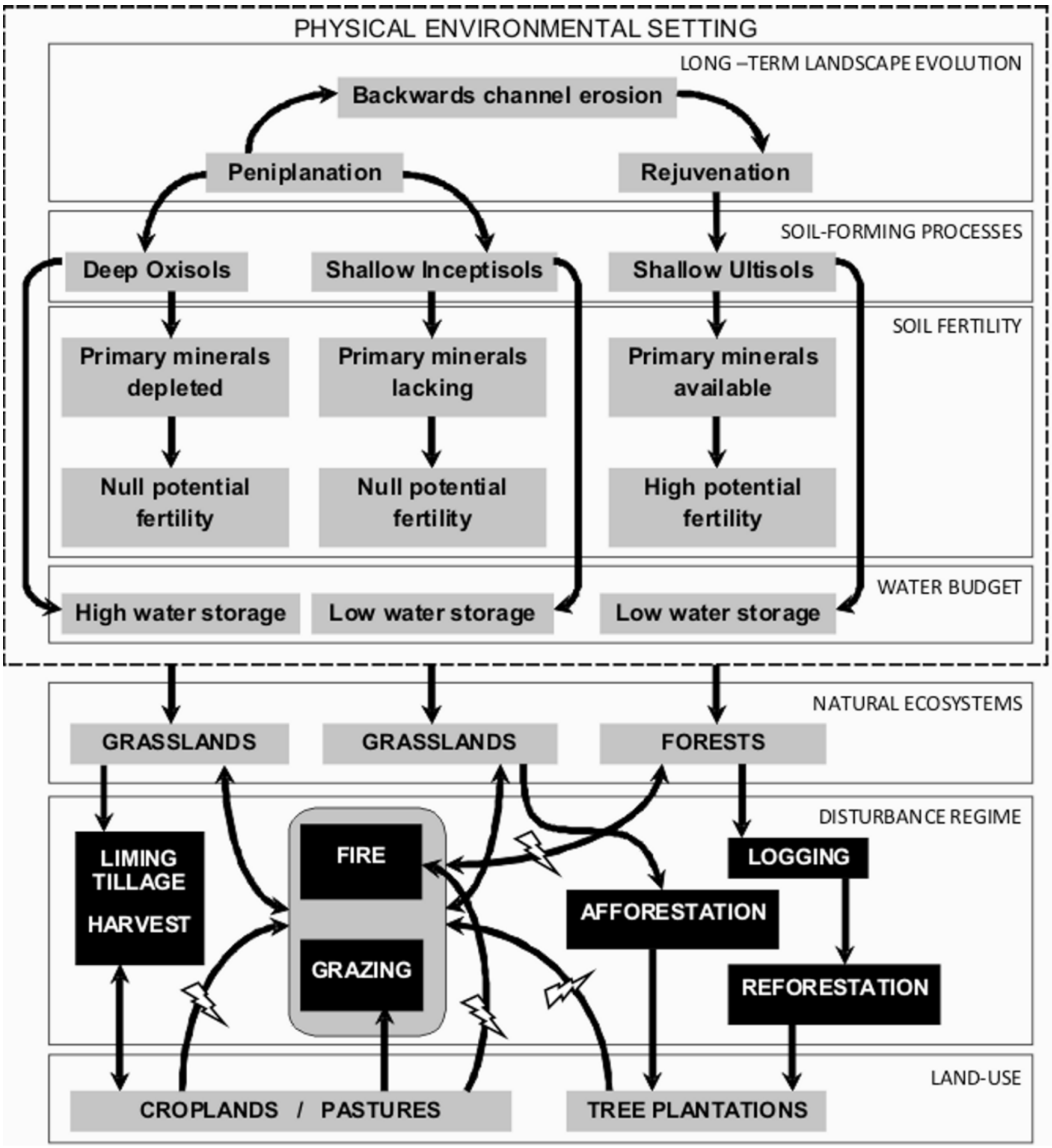

Table 7. Conceptual model relating environmental factors, land use and natural ecosystems, in northern Rio Grande do Sul. The arrows represent positive and ( ) negative interactions.

in time and space. Yet, a similar mechanism of forest expansion could also apply in this case, with forests developing along ravines dissecting the colluvial slopes, mostly overtop by ultisols, or around mid-slope wellsprings. Concentrated erosion would provide grass-free sites for forest elements to takeover and the new hydrologic regime would supply nutrients otherwise scanty.

The setting apart of grasslands and forests along topographic and soil sequences strongly suggest that water and nutrients may be issues underpinning the vegetation mosaics, being forest more demanding on both resources. Given the moist climate prevailing over the entire tablelands, we may give more weight to nutrients than to water availability, though water fluxes through the soil also determines nutrient fluxes. The fact that recurrent fires, either natural or human induced, favour grasslands over forests is undeniable since it eliminates forest seedlings from the grassland matrix as well as the young trees growing at the edge of the forest patches. Cattle trampling and browsing would also have the same effect. Yet, we call the attention to the fact that vegetation fires are primarily a by-product of the widespread occurrence of grasslands. As a matter of fact, it has been shown that in tropical savannas despite the high frequency of fire, the woody component may expand at the expense of the grassy layer (Dauget and Ménaut 1992, Silva *et al*. 2001). We hypothesize that these disturbance-related factors are decisive at the local scale and only wherever the geomorphic dynamics has not yet taken over ecosystems turnover. The primary driver for the spatial disjunction of both types of ecosystems, at the regional and local, would remain nutrient availability.

CONCLUSIONS

Land use has been somewhat obscuring natural vegetation boundaries, even though croplands, actually the most extensive form of land use, do concentrate on deep soils formerly in the dominion of grasslands. Forestry is more eclectic since it extends over forestlands and grasslands as well. However, the picture so far described tells about a rather close relationship among the distribution of the major vegetation types and land-uses with soils and terrain-forming processes. In this picture, the grasslands prevail where terrain and soil features suggest there are the remnants of ancient peniplanation surfaces. Forests, on the other hand, seem to dominate wherever geomorphic agents have rejuvenated the landscape. This being so, we suggest that ecosystem patterning processes in the basaltic plateau are similar to those occurring in the tropical lowlands where forests and savannas coexist (Sarmiento and Pinillos 2001). However, the fact is that in a realistic model aimed to explain the current development of the forest-grassland pattern, fire disturbance cannot be ignored for it has been concomitant to the forest expansion process throughout the second half of the Holocene. Fire frequency and intensity have to be understood as functional attributes of the grasslands, emerging from the interaction of biological, soil and climatic drivers. Likewise, the impact of the fire regime on the ability of forests to expand need to be understood in relation with forest functional attributes, as diverse as these can be given the variety of physiognomic and phenological traits that forests display and the environmental complexity under which they occur. The same would apply to other disturbances, such as grazing and trampling by domestic herbivores.

Our research shows that the high-level drivers of the land cover - land use mosaics, characteristic of the basaltic tablelands of northern Rio Grande do Sul, Brazil, can be identified in relation to geomorphic phenomena controlling water and nutrient supply, soil evolution and human action. Terrain evolution and spatial vegetation patterning are two major dimensions of landscape dynamics, though these are rarely studied in relation to one another. Our approach emphasizes the importance of terrain-forming processes on the comprehension of the spatial dynamics of the vegetation, pointing out the relevance of understanding the effect of climate change on the geomorphic dynamics in order to interpret the history of the vegetation in a given region and the distribution of contrasting ecosystems. We conclude that this approach is a fruitful research avenue through which complex vegetation patterns may be understood in ecological terms, in any situation where vegetation mosaics imprint the whole landscape**.**

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