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Habitat dynamics in subtropical South America: Socioeconomic determinants and landscape patterns at a forest-grassland ecotone

Dinâmica de habitats na região subtropical da América do Sul: determinantes socioeconômicos e padrões de paisagem em um ecótono floresta-campo

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Abstract

We investigated landscape structure and spatialpatterns of natural grasslands and Atlantic Forests in southern Brazil in 1984, 1994, and 2005. The studied region is a highland grassland disjunct region (*campos de cima da serra*) surrounded by forests. We asked: (a) was there an intensification of habitat loss, fragmentation, and isolation of the Atlantic forest or grassland, within the highland ecotonalzone? (b) What was the degree ofconnectivity/isolation of the patches? (c) Was there any pattern of grassland loss related to moisture/microtopography? (d) Did agroeconomic activities influence landscape patterns and land use change? We analyzed Landsat remotely sensed information to characterize the land use and land cover, also considering subdivision into eight agroeconomicregions. Results showed that the area occupied by agriculture suffered a strong expansion along with exotic tree plantations, at the expense of grasslands, which suffered marked loss and fragmentation. Grassland destruction was biased towards humid areas in valleys between relief undulations. Forests expanded as a network of small patches in close contact with other land uses. Land cover differed significantly among agroeconomic regions, suggesting that conservation measures need to contemplate both forest and grassland ecosystems and socioeconomic distinctions as well.

Keywords: Araucaria forest, fragmentation, Pampa.

Resumo

Investigamos a estrutura da paisagem e padrões espaciais de campos nativos e de florestas Atlânticas no sul do Brasil em 1984, 1994 e 2005. A região estudada é um enclavede campo cercado por florestas. Perguntamos: (a) houve intensificação da perda de habitat, fragmentação e isolamento da floresta Atlântica ou do campo? (b) Qual foi o grau de conectividade/isolamento dos fragmentos? (c) Houve algum padrão de perda de campo relacionada à umidade/microtopografia? (d) O padrão de atividades agroeconômicas influencia a estrutura da paisagem e mudanças no uso do solo? Analisamos imagens Landsat de sensoriamento remoto para caracterizar o uso e cobertura do solo, considerando também a subdivisão da paisagem em oito regiões agroeconômicas. Os resultados mostraram que a área ocupada pela agricultura sofreu forte expansão, juntamente com plantações de árvores exóticas, em detrimento do campo, que sofreu perda e fragmentação acentuada. A destruição do campo foi mais acentuada em áreas úmidas situadas em vales entre ondulações do terreno. As florestas sofreram expansão como uma rede de pequenas manchas em estreito contato com outros usos do solo. A cobertura do solo diferiu significativamente entre as regiões agroeconômicas, sugerindo que medidas de conservação precisam contemplar ambos os ecossistemas, assim como distinções socioeconômicas.

Palavras-chave: floresta com araucárias, fragmentação, Pampa.

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Introduction

Habitat loss and fragmentation are regarded as major threats to biodiversity conservation, producing landscapes with reduced connectivity, and degraded native vegetation that trigger extinction cascades, especially if keystone species or entire functional groups of species are lost (Fischer and Lindenmayer, 2007). One of the main drivers of habitat loss is the expansion of the agricultural frontier, which also sometimes produces the redistribution of vegetation cover over entire regions (Overbeck *et al.*, 2007). In recent decades, the Brazilian agricultural production suffered a marked increase (Mantelli, 2006), mainly due to increased production of annual cultures through both agricultural expansion and increased productivity (Overbeck *et al.*, 2007). Accordingly, this agricultural expansion has been accompanied by native habitat loss (Cordeiro and Hasenack, 2009) and redistribution in southern South American landscapes (Baldi and Paruelo, 2008; Hansen *et al.*, 2013; Hendges *et al.*, 2012; Scariot *et al.*, 2015). Given the complexity of the interaction between human activities and native ecosystem distribution across landscapes, it is of paramount importance to gain detailed knowledge on the spatial patterns of both habitat destruction and remnant vegetation distribution (Fischer and Lindenmayer, 2007).

In subtropical South America, a large ecotonal area occurs near the parallel 30ºS where the Atlantic Forest and the Pampa grassland ecoregions meet. Southern Atlantic forests comprise themselves a biogeographic convergence zone between lowland rainforests, upland mixed conifer-hardwood forests dominated by *Araucaria angustifolia*, and semideciduous forests (Gonçalves and Souza, 2014). The Pampa grasslands (known as *campos* in Brazil) are biodiversity rich ecosystems that occur as a continuous block that covers the lowlands over the lower half of the Rio Grande do Sul Brazilian state and all Uruguay (Bilenca and Miñarro, 2004), as well as disjunct areas in northern Rio Grande do Sul, Santa Catarina, and Paraná (Overbeck *et al.*, 2007).Across the Rio de La Plata larger region (Baldi and Paruelo, 2008), and the Brazilian state of Rio Grande do Sulin particular (Cordeiro and Hasenack, 2009), significant reductions in grassland cover in the last decades of the 20th century have been measured. This loss can be related to agricultural expansion, but also to increased exotic tree plantation areas (Brockerhoff *et al.*, 2008; Hansen *et al.*, 2013; Souza *et al.*, 2013). The Pampa grasslands biological diversity is differentiated along moisture/microtopographic gradients (Focht and Pillar, 2003), and hence grassland loss should affect distinct sets of species depending on the spatial distribution of land conversion. Forested areas, on the other hand, seem to have expanded (Duarte *et al.*, 2006;Hansen *et al.*, 2013; Hendges *et al.,* 2012; Scariot *et al.*, 2015), possibly for socioeconomic reasons related to rural exodus and ageing smallholder rural populations (Schneider, 1994). Up to now, land use changes in southern Brazil have been poorly documented compared to other regions of Brazil, and the socioeconomic drivers of these changes have scarcely been investigated (see Naumov, 2005 for a general review).In the transitional forest-grassland region of southern Brazil (northern Rio Grande do Sul), small-scale family agriculture concentrates on beans, manioc, pork, and chicken production, and coexists with extensive business agriculture concentrated on soy, corn, tobacco, wheat, and cattle ranching (Rio Grande do Sul, 2012). Current wet climatic conditions with no marked annual dry season are favorable to forest expansion over grasslands, which indeed has occurred in the last 4,000 years (Behling *et al.*, 2004).

Here we investigated temporal changes in landscape structure and spatial patterns of natural grasslands and forests in different years (1984, 1994 and 2005) in northeastern Rio Grande do Sul, southern Brazil. The studied region is a highland grassland disjunct region (*campos de cima da serra*) surrounded by mixed conifer-hardwood, semideciduous, and lowland rainforests (Gonçalves and Souza, 2014). We addressed the following questions: (a) was there an intensification of habitat loss, fragmentation, and isolation of the Atlantic forest or grassland, within the highland ecotonal zone between 1984 and 2005? (b) What was the degree of connectivity/isolation of the patches of Atlantic forest and grassland within the ecotonal zone between 1984 and 2005? (c) Was there any pattern of grassland loss related to the moisture/microtopographic gradient? (d) Did agroeconomic activities influence landscape patterns and land use change?

Material and methods

Study area

The studied forest-grassland ecotone covers an area of ca. 300,000 Km^2 in southern South America and lies entirely within the Brazilian state of Rio Grande do Sul, near the parallel of latitude 30ºS (Figure 1). This region is characterized by differences in geomorphology and geological history (Streck *et al.*, 2008), leading to strong gradients in topography and soil characteristics. A basaltic mountain range (the *sul-riograndense* highlands) forms an arch of descending altitudes from the northeastern plateau (max. elevation ca. 1300 m) to lower southwestern undulated terrains. A NE-SW diagonal of flat lowlands of sedimentary origin, known as the Central Depression, borders the inner side of the highland arch. Soils vary in fertility from acid Cambisols in the highlands, to Argisols and Neosols on the slopes of the highlands, and Latosols on the northwestern hilly lowlands of the Uruguay River valley (Streck *et al.*, 2008).

Climate is classified as Köppen-Geiger type Cf, a temperate humid climate type, lacking a true dry season (Peel

Figure 1. Distribution of the Atlantic Forest and Pampa ecoregions in South America, and the location of the study area (square).

et al., 2007). Climate type Cfb (warm summer) is found in the higher areas of the plateau, where winter temperatures average 9ºC, average summer temperatures do not exceed 22°C, and frosts are common (Kuinchtner and Buriol, 2001). Climate type Cfa (hot summer) prevails throughout the region, with average summer temperature above 22°C. Annual precipitation varies from 1,351 mm to 2,091 mm. Apart from a limited occurrence of Rainforests of tropical origin in the eastern slopes, most forests in the region are Eastern Mixed Forests, a type of conifer-hardwood forest dominated by the conifer *Araucaria angustifolia* with hardwood species from both tropical and temperate origins (Gonçalves and Souza, 2014). They cover mainly the slopes and also occur as patches of varying sizes and conservation status embedded in seminatural grasslands in the flat upper areas (Souza *et al.*, 2012). Grasslands form a mosaic with mixed forests in the northern half of Rio Grande do Sul and in the states of Santa Catarina and Paraná (Overbeck *et al.*, 2007). Larger land ownerships (> 500 ha) concentrate in the highest northeast of the studied area, where corporate livestock ranching predominates over agriculture (SCP, 2002). Smaller land ownership predominates westwards and southwards, where family agriculture becomes increasingly important (SCP, 2002). Despite the relatively limited size of farms in the western part of the state, business-oriented intensive plantations correspond to an important proportion of the agricultural production, mainly soy (Rudorff *et al.*, 2007; Gusso *et al.*, 2012). Eucalypt and pine plantations are important land covers in the plateau (Overbeck *et al.*, 2007).

Several physiographic subunits can be distinguished according to geomorphology, soils, drainage, and physiographic and vegetation characteristics: the Upland Grasslands (*campos de cima da serra*), Medium Plateau, Upper Slope, Lower Slope, Central Depression, and Coast (Fortes, 1959). We focused on an area of 1,048.6 Km^2 centered on the Upland Grasslands and the surrounding Northeastern Upper Slope and Northeastern Down Slope (Figure 1) as these areas include the main environmental (topographic and vegetational) and land-use history gradients.

Land cover and land-use characterization

We analyzed Landsat 5 Thematic Mapper (TM) remotely sensed information with a spatial resolution of 30 m (1:50,000 scale) to characterize the land use and land cover of a 1,048,656 Km^2 area (from 27°57›32»S to 29°47›9»S; from 51°51›18» to 50°17›53»W)for 1984, 1994 and 2005. Already registered Landsat scenes were obtained from the INPE (Spatial Research National Institute, Portuguese acronym) website (http://www.dgi.inpe.br/CDSR/, row/path 221/80 in all cases, Universal Transverse Mercator projection system, zone 22, datum WGS84). Only images with up to 10% cloud cover were used. We then performed atmospheric corrections using the Fast Line-of-sight Atmospheric Analysis of Spectral Hypercubes (FLAASH) module of ENVI. FLAASH is a first-principles atmospheric correction tool that corrects wavelengths in the visible through near-infrared and shortwave infrared regions, up to 3 µm (Yuan and Niu, 2008).Radiometric calibration was not applied to the satellite imagery because differential illumination was not visible and atmospheric influences were very low (Bishop *et al.*, 1998). Land cover and land use maps were obtained by supervised interpretation of the Landsat scenes using the ENVI 4.5 GIS (Exelis Visual Information Solutions, Boulder, Colorado). We mapped five land cover and land use classes: (i) native forest: old growth and secondary mixed and rain forest remnants,(ii) grasslands: seminatural grasslands, (iii) agriculture: annual and perennial crops and agricultural land in preparation for farming, (iv) tree plantations: eucalypt or pine plantations, and (v) urban areas. To optimize the interpretation urban and silvicultural areas were removed from images before classification due to reduced sample size (Mather and Koch, 2011).

We quantified landscape structure, i.e., composition and configuration, for the two study intervals using five indices because no single metric can capture the complexity of the spatial arrangement of patches (Riitters *et al.*, 1995). The Area (CA), Average Area (Area MN), Edge Contrast Weigh (CWED), Aggregation (AI), and Interspersion and Juxtaposition (IJI) indices were calculated using FRAGSTATS 3.3 (McGarigal and Marks, 1995). This software calculates spatial pattern metrics, such as number of patches, shape indices and forest interior metrics, which describe landscape pattern. The Edge Contrast Weighindex (CWED) standardizes edge to a per unit area basis that facilitates comparison among landscapes of varying size. The interspersion index (IJI) measures the extent to which patch types are interspersed; higher values result from landscapes in which the patch types are well interspersed, whereas lower values characterize landscapes in which the patch types are poorly interspersed. The Edge density index (ED) standardizes edge to a per unit area basis that facilitates comparisons among landscapes of varying size. For the calculation of Edge Density index, human-related classes (urban, silviculture, and agriculture) weighted 1 and natural classes (forests, grasslands, and water) weighted zero. For the six classes, we calculated landscape pattern metrics for the whole landscape, and for the upland grasslands separately. In the analyses of upland grasslands, we discriminated between Northern and Southern upland grasslands, since this physiographic region is divided by a northeast-southwest forested depression (Figure 2). Due to the commonness of small forest fragments in the study area (Souza *et al.*, 2012) and their prevalence in the Atlantic Forest domain (Ribeiro *et al.*, 2009), we did not exclude small polygons from analyses.

We used the normalized difference moisture index (NDMI) to distinguish between waterlogged-prone grasslands (*banhados*) from well drained grasslands. Although less popular than other indexes related to vegetation cover like the NDVI, which measures vegetation cover, the NDMI has been shown to be highly correlated with the foliage water content and fraction of dead leaf material (Hunt

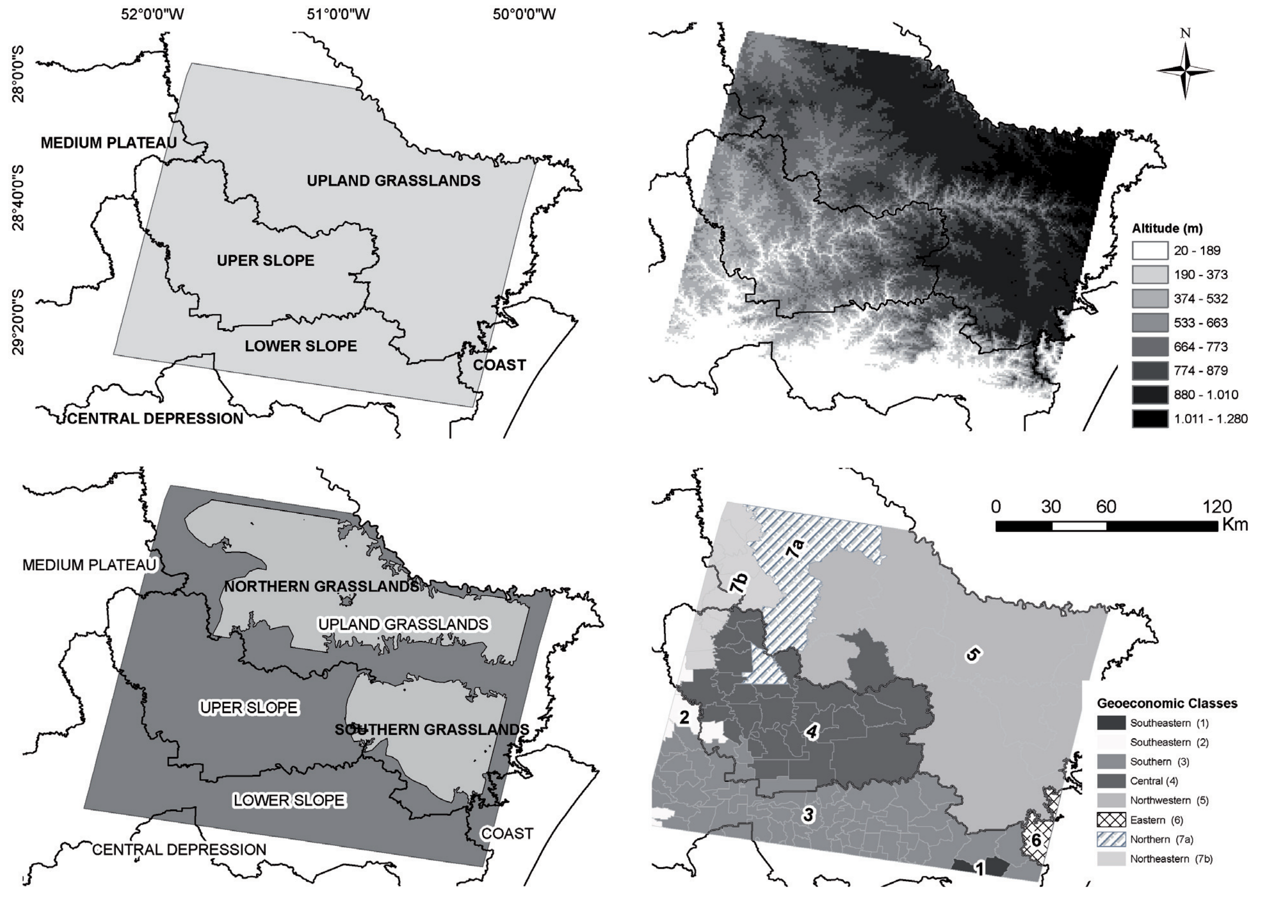

Figure 2. Studied landscape and physiograpic units (A), elevation variation (B), grassland occurrence (C), and agroeconomic classes (D) found therein.

et al., 1987), constituting a better moisture content indicator than the NDVI (Hardisky *et al.*, 1983; Gao, 1996; Wilson and Sader, 2002). This is due to increased sensitivity to water absorption originated by the contrast between the near and medium infrared bands, since the medium infrared is less influenced by atmospheric effects (Wilson and Sader, 2002). It is worth noting that the NDMI is mainly correlated with moisture retained on the vegetation more than soil moisture. The NDMI is the normalized ratio of the shortwave (TM band 5) and near infrared (TM band 4) bands, and was calculated in ENVI. It generates moisture classes with values proportional to vegetation moisture. In order to consider human activities heterogeneity, each municipality within the studied polygon was classified into one of the eight agroeconomic regions proposed for the state of Rio Grande do Sul by Brum Neto *et al.* (2007). The classification of Brum Neto *et al.* (2007) considered the main agricultural and animal products of each region as well as the land ownership structure and agroeconomic dynamism: (1) pecuary and rice fields, (2) corn and tobacco, (3) corn, tubers and fruit production along with chicken and pork production, (4) grape, (5) apple and cattle, (6) banana, pineapple, and palm heart, (7a) soy and wheat along with cattle, and (7b) soy and wheat along with chicken. All eight agroeconomic classes were represented in the studied landscape (Figure 2).

Landscape analysis

Log-linear analyses (Sokal and Rohlf, 1995) were used to determine whether land use and grassland moisture differed significantly between the studied periods. For land use agroeconomic classes and time interval were also used as explanatory variables. The significance of the explanatory variable is analysed by examining the increase in χ^2 (i.e. $\Delta\chi^2$) when it is excluded from a model that included it. The level of significance to reject the null hypothesis was set at $p < 0.05$ in all tests. The statistical analyses were carried out with the software SYSTAT 12 (Systat Software Inc.).

Results

In 1984, most of the studied landscape was occupied by grasslands, mainly in the uplands (Table 1). Forests occupied a much smaller area of the region and were distributed on the slopes of the sul-riograndense highlands, also occurring on the uplands as a network of patches and corridors (Figure 3). Agricultural areas represented a small part of the studied area and were more abundant over the northwestern part of the image as well as in the Central Depression. Exotic tree plantations were scattered on the

Table 1. Class area of natural and human activities in the northeastern portion of the sul-riograndense highlands, southern Brazil, from 1984 to 2005.Figures correspondent to water bodies not shown.

Year	Grassland	Forest	Agriculture	Sylviculture	Urban
1984	79.00	13.90	4.90	1.30	0.16
1994	22.70	11.00	63.00	2.40	0.17
2005	20.00	33.00	43.00	2.60	0.26

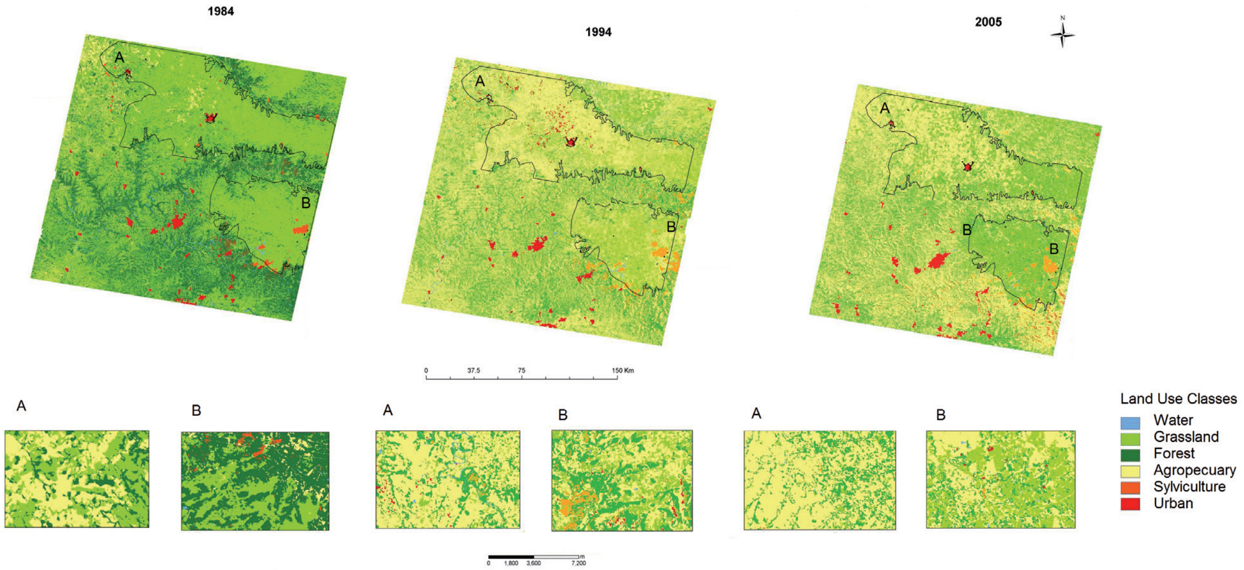

Figure 3. Total landscape structure in 1984, 1994, and 2005 in southern Brazil. Insets show examples of landscape structure at a smaller scale. (A)agriculture, (G)seminatural grasslands, (F) native forest, (S)sylviculture of exotic tree species, (U) urban.

plateau. Agriculture was the most scattered of the land cover classes, with 156885patchesof 1.7 Km^2 in average. Forest patches were also numerous (N = 115642), with 9.5 Km^2 in average. Grasslands occurred as relatively large patches (average = 19.8 Km^2).

From 1984 to 1994 the area occupied by agriculture suffered a strong expansion, increasing by 129.5%, along with exotic tree plantations, the area of which increased by 184.6% (Table 1, Figure 4). These expansions occurred mainly at the expense of grasslands, which suffered a strong reduction (71.1%), and forests (reduction of 24.7%).From 1994 to 2005 agriculture areas suffered a 31.5% contraction, accompanied by a strong forest expansion (303.5%) over both former agricultural areas and grasslands. The net result was a contraction of grasslands, which reached 2005 with 25.5% of its extension in 1984. Urban areas increased markedly over the whole 21-year period (162.5%).Over the entire study area and period, grasslands became increasingly fragmented, with 86,647 grassland patches of average 19.8 Km^2 in 1984 rising to 116,495 patches of average 4.1 Km^2. Forest patches increased from 115,642 of average 9.5 Km^2 to 223,640 of average 3.9 Km^2.

More detailed analyses of landscape cover changes in the Upland Grasslands sub-region revealed particular trends. In this sub-region, the increase in landscape cover by agriculture from 1984 to 2005 was not accompanied by increases in this land use class mean patch size, while edge contrast, aggregation, and juxtaposition increased very modestly (Figure 4). This indicates that agriculture increased by the augmentin the number of relatively small cultivated patches that coalesced to some extent. A similar pattern was found for exotic tree plantations. Grassland patches increased markedly in mean size and edge contrast (contact with different land use patches). Forest expansion was not accompanied by important increases in forest patch size or aggregation, but edge contrast and patch juxtaposition increased markedly. This indicates that forests expanded as a network of small patches in close contact with other land uses. Urban patch size decreased despite steady increase in total urban area. In the Upland Grasslands vegetation moisture, as measured by the NDMI index, was significantly reduced ($G = 592875.97$, gl = 26, $P < 0.0001$). This reduction appeared in the increase in the area of the first NDMI class, which represents the driest patches, as well as in the decrease in the area of the largest classes representing the moister patches (Figure 5).

The distribution of landscape cover classes was markedly different between agroeconomic regions in 1984. The Tropical Fruit and Palm Heart region was predominantly forested, the Apple and Cattle and the Soy, Wheat and

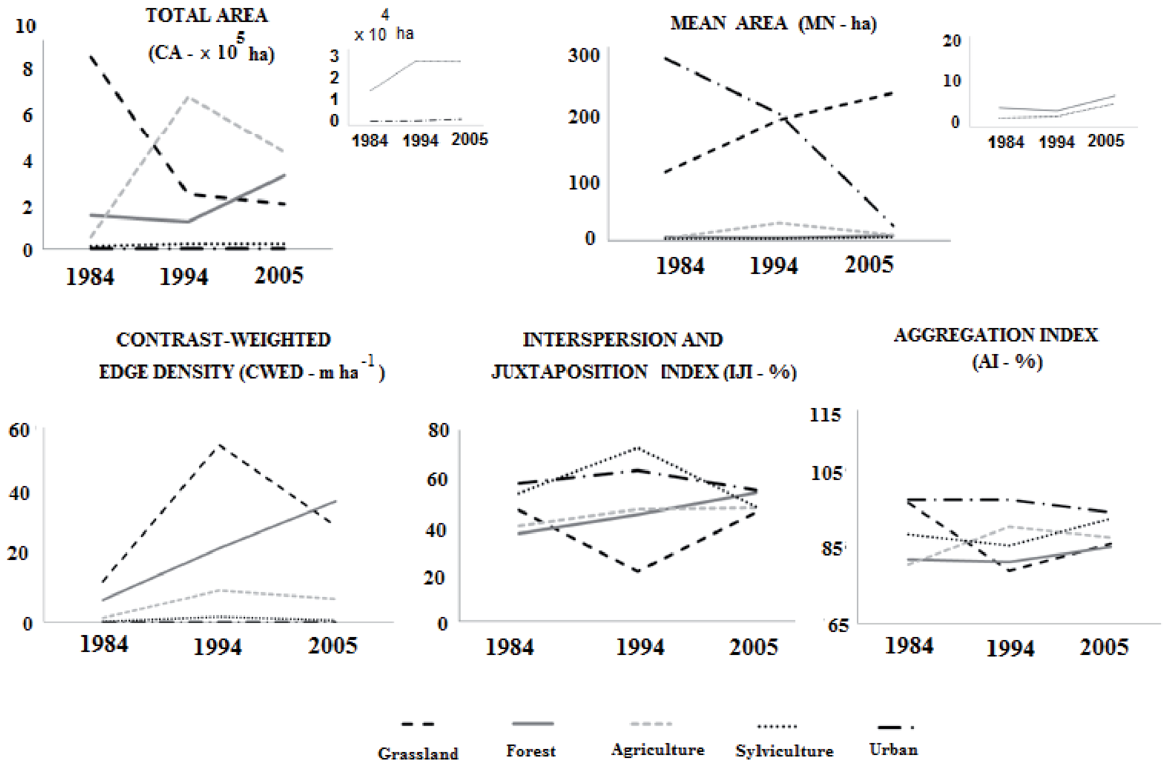

Figure 4. Landscape metrics calculated for different land use classes in the Upland Grasslands, southern Brazil, from 1984 to 2005.

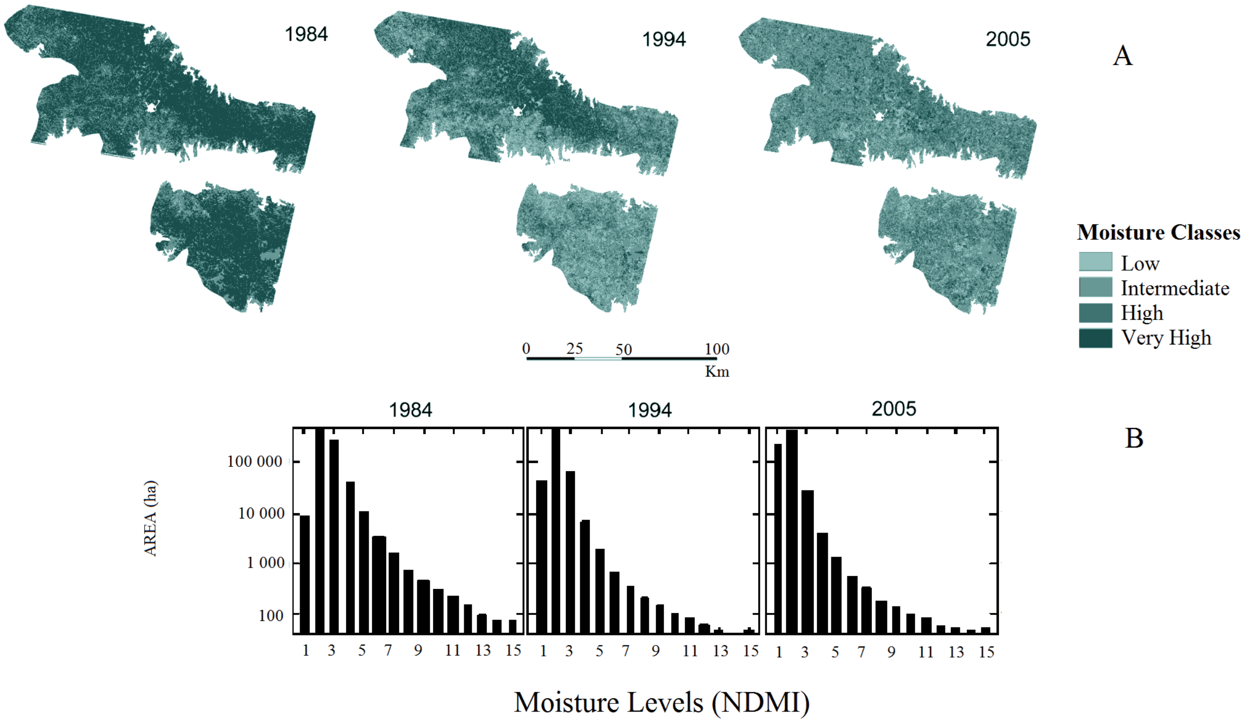

Figure 5. Moisture dynamics in the Upland Grasslands in southern Brazil from 1984 to 2005 as depicted by the NDMI index. (A) Landscape scale distribution of grouped NDMI classes. (B)Frequency distribution of the NDMI moisture classes.

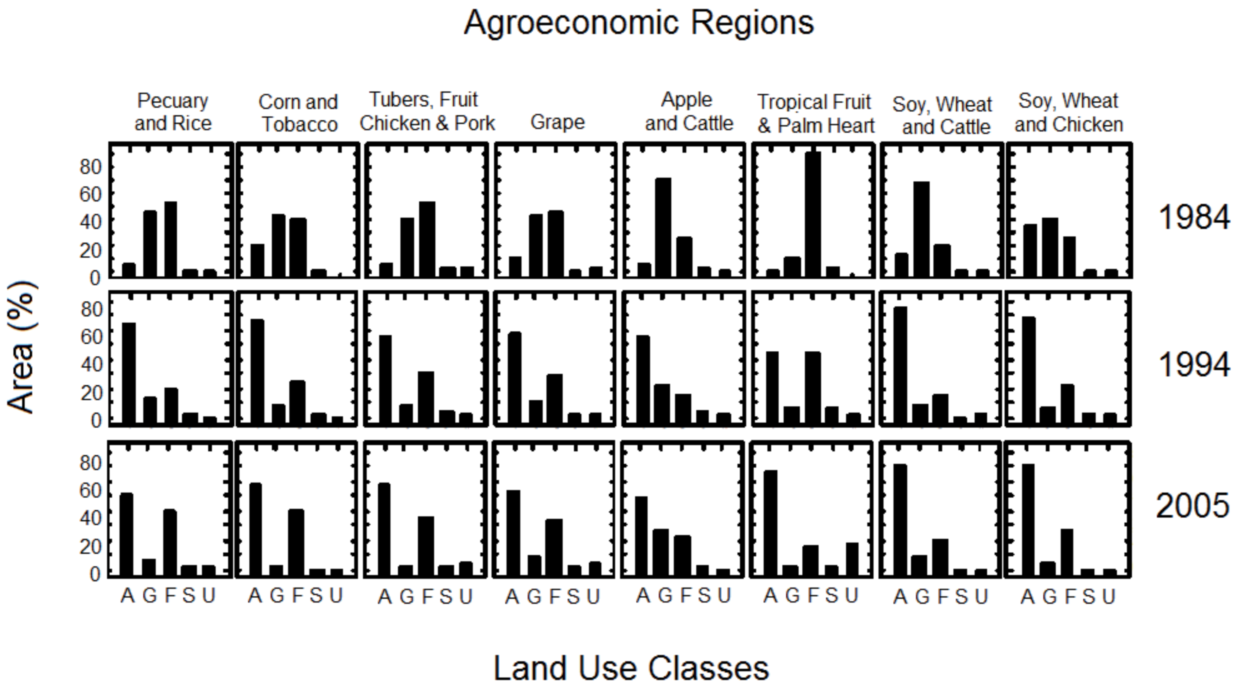

Figure 6. Land use patterns in different agroeconomic regions in the studied landscape in southern Brazil from 1984 to 2005.

Cattle were predominantly grassland regions, while the remaining regions presented balanced proportions of forest and grassland. Landscape structure differed between agroeconomic regions and between time intervals (loglinear model, $\chi^2 = 89{,}120.61$, gl = 40, $p < 0.0001$, Figure 6). Agriculture cover increased in all agroeconomic regions, and the majority of this increase occurred from 1984 to 1994, with small reductions in the Pecuary and Rice and Apple and Cattle regions from 1994 to 2005. Agricultural expansion was accompanied by some forest cover reduction in the Pecuary and Rice, Corn and Tobacco, Tubers, Fruit, Chicken and Pork, Grape and Tropical Fruit and Palm Heart regions from 1984 to 1994. This pattern was reversed from 1994 to 2005, however, in most of these regions, which showed forest expansion. Grassland cover reduction occurred in all agroeconomic regions. It was particularly strong in the regions where seminatural grasslands were originally the dominant land cover, such as the Pecuary and Rice, Apple and Cattle, and Soy, Wheat and Cattle regions, as well as in originally forest dominated regions as the Grape region and the Tubers, Fruit, Chicken and Pork region. Land cover changes were expressive enough to alter the environmental profile of most regions from previously dominated by forests or grasslands to agricultural dominance.

Discussion

Grassland destruction

South Brazilian grasslands represent the northern limit of the Pampa ecoregion (Bilenca and Miñarro, 2004), a native ecosystem that occupy some 13.7 million ha and support from 3,000 to 4,000 phanerophytes but is poorly protected (Overbeck *et al.*, 2007). The main pattern emerging from our results is the large-scale grassland loss to expanding agriculture, followed by the redistribution of forest cover over large portions of the studied landscape. Three of the eight agroeconomic regions studied (Apple and Cattle, Soy, Wheat and Chicken, and Soy, Wheat, and Cattle) reached 2005 near the threshold of natural vegetation cover of 40% suggested by Metzger and Décamps (1997) to buffer fragmentation and isolation effects. If we consider the grassland and forest vegetation types separately, however, five of the eight regions reached 2005 with less than 40% of the initial grassland cover (Pecuary and Rice, Corn and Tobacco, Tubers, Fruit, Chicken, and Pork, Soy, Wheat and Cattle, and Soy, Wheat and Chicken), and the Tropical Fruit and Palm Heart region failed this threshold regarding forest cover.

A possible drawback in the grassland destruction we found could be due to measurement error related to the distinction between burned grasslands and plowed soil in preparation for seeding. Grassland periodic burning is a common management practice to improve pasture for the cattle (Quadros and Pillar, 2001). There are grounds, however, to believe that such error, if present, was not responsible for the estimated habitat loss. During the studied period the Brazilian agricultural production in general, and that of the Rio Grande do Sul state in particular, suffered a marked increase (Mantelli, 2006). Overbeck *et al.* (2007) estimated that southern Brazilian grasslands were reduced by ca. 25% from 1970 to 1996 due to the expansion of soybean, corn, wheat, and rice cultures. Accordingly, Baldi and Paruelo (2008) and Cordeiro and Hasenack (2009) estimated significant reductions in grassland cover in the general Pampa region and in the Rio Grande do Sul Northern Campos in the last decades of the 20th century. The fact that the majority of grassland destruction we found took place from 1984 to 1994 corresponds to the expansion of the agricultural frontier in this period (Mantelli, 2006), which suffered a halt in the first years of the 21th century (Rio Grande do Sul, 2012). It is worth noting that the grassland habitat destruction trend found here may have continued in more recent years, because the agricultural production regained strength after 2005 (Rio Grande do Sul, 2012; but see Scariot *et al.*, 2015).

Grassland replacement was not spatially homogeneous. It was a directional process occurring more intensely in the northern part of the Upper Grasslands, the slopes of the highlands, and in the Central Depression than in the southern part of the Upper Grasslands. This resulted from the fact that agricultural activity has expanded from the northwestern and western regions of Rio Grande do Sul, where annual culture planted area has been growing since the 1940's (Mantelli, 2006). While the southern Upper Grasslands have been less intensely converted to agriculture, it is in this area that exotic tree plantations, mainly *Pinus* spp., have expanded most. As in the study region, worldwide exotic tree species are widely planted under short rotation cycles (Brockerhoff *et al.*, 2008; Hansen *et al*., 2013), but they are poor habitats for most of the native fauna and flora (Fonseca *et al.*, 2009), and have been shown to reduce plant diversity in the surrounding grasslands due to cattle exclusion (Souza *et al.*, 2013).Furthermore, *Pinus*s pp. are invasive alien species and constitute a severe threat to the conservation of native grassland species and communities (Guadagnin *et al.*, 2009).A consequence of the agricultural expansion in a northwestern-southern arch is that the southern part of the Upper Grasslands, in the Apple and Cattle agroeconomic region remains as a refuge for grassland ecosystems in the region, as also pointed out by Cordeiro and Hasenack (2009). The much needed creation of grassland conservation areas (Overbeck *et al.*, 2007) should thus target this region, which is recognized by the Brazilian federal environmental agencies as a priority area for conservation (Brasil, 2000).

An important characteristic of the grassland removal process was its concentration on the wet grasslands (*banhados*) found in the valleys between terrain undulations over the Upland Grasslands. This pattern has conservation implications because wet grasslands constitute a floristically distinct habitat from grasslands on the slopes (Focht and Pillar, 2003) and harbors habitat specific bird and mammal species (Bencke, 2009). The specific loss of wet grasslands is not attributable to climate trends. Annual rainfall has been shown to have significantly increased in southern Brazil in general, and in the study region in particular from 1930 to 2005 (Pinheiro *et al.*, 2013). The spread of agricultural activities over grasslands prioritizing the network of low wet habitats helps explain the increased fragmentation of grasslands that accompanied its areal reduction (as in Baldi and Paruelo, 2008). The creation of a large number of grassland fragments poses important conservation issues since the impacts of human-induced disturbances common in the region, such as fire (Overbeck *et al.*, 2006), are expected to be enhanced. Extinction cascades are particularly likely to occur since they have been registered in landscapes with low native vegetation cover, low landscape connectivity, degraded native vegetation and intensive land use in modified areas, especially if keystone species or entire functional groups of species are lost (Fischer and Lindenmayer, 2007).

Forest expansion

Our results showed that agricultural expansion was not the only factor responsible for grassland reduction. At the same time agricultural activity expanded from the west, Mixed and Semideciduous Atlantic Forests also expanded in the Upland and Slope physiographic regions of the studied landscape. This result is an exception to the global trend of subtropical forest loss to forestry (Hansen *et al*., 2013) but agrees with regional findings (Cordeiro and Hasenack, 2009; Hendges *et al.,* 2012; Scariot *et al.,* 2015). It may seem contradictory with the grassland destruction by agricultural expansion we also registered. Two distinct processes may help explain forest expansion. At a large scale, current wet climatic conditions with no marked annual dry season are favorable to forest expansion over grasslands, which indeed has occurred in the last 4,000 years (Behling *et al.*, 2004). At a more regional scale, improving living conditions and increased agricultural mechanization have led to land concentration (in the western parts of the studied region, Schneider, 1994; Mantelli, 2006) and rural exodus (Naumov, 2005; Schneider, 1994). The marked increase in the area occupied by cities during the studied period is a direct consequence of the rural exodus (Naumov, 2005). It is important to highlight that the Tropical Fruit and Palm Heart agroeconomic region was an exception to this dominant trend, and suffered a marked net forest loss in the studied period. In this region forests were replaced by agriculture, mainly sugar cane and banana (Rio Grande do Sul, 2012), accompanied by a marked increase in urban areas related to touristic activities.

Forests expanded from fragments over abandoned agricultural fields mainly in smallholder family farming units belonging to ageing families of German or Italian ancestry (Schneider, 1994) in the southern Upland Grasslands and surrounding slopes. Southern Atlantic forests have been shown to colonize grasslands through direct succession from fragment edges and natural patches under grazing and fire exclusion (Oliveira and Pillar, 2005) or through nucleation around isolated *Araucaria angustifolia* trees growing in grasslands (Duarte *et al.*, 2006).The conservation status of small forest patches in the southern extreme of the Atlantic Forests, however, is generally impaired by cattle grazing (Souza *et al.*, 2010) and other non-sustainable uses (Souza *et al.*, 2012). Biodiversity conservation has been shown to be much increased, however, under minimally protected areas (Souza *et al.*, 2012). Overall, our results point to the need of an integrated large-scale strategy allowing for the simultaneous conservation of the biodiversity priority areas (Brasil, 2000) in both grasslands and forests in this large biogeographic transition region.

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References

BALDI, G.; PARUELO, J.M. 2008. Land-use and land cover dynamics in South American Temperate grasslands. *Ecology and Society*, **13**(2):6. http://dx.doi.org/10.3759/tropics.17.99

BEHLING, H.; PILLAR, V.D.; ORLÓCI, L.; BAUERMANN, S.G. 2004. Late Quaternary Araucaria forest, grassland (Campos), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **203**(3-4):277-297. http://dx.doi.org/10.1016/S0031-0182(03)00687-4

BENCKE, G. 2009. Diversidade e conservação da fauna dos Campos do sul do Brasil. *In:* V.D.P. PILLAR; S.C. MÜLLER; Z.M. de S. CASTILHOS; A.V.A. JACQUES (org.), *Campos sulinos: conservação e uso sustentável da biodiversidade*. Brasília, Ministério do Meio Ambiente, p. 101–121.

BILENCA, D.; MIÑARRO, F. 2004. *Identificación de áreas valiosas de pastizal en las pampas y campos de Argentina, Uruguay y sur de Brasil (AVPs)*. Buenos Aires, Fundación Vida Silvestre Argentina, 323 p.

BISHOP, M.P.; SHRODER, J.F. JR.; HICKMAN, B.L.; COPLAND, L. 1998. Scale-dependent analysis of satellite imagery for characterization of glacier surfaces in the Karakoram Himalaya. *Geomorphology*, **21**(3-4):217-232. http://dx.doi.org/10.1016/S0169-555X(97)00061-5

BRASIL. 2000. *Avaliação e ações prioritárias para a conservação da biodiversidade da Mata Atlântica e Campos Sulinos*. Brasília, Ministério do Meio Ambiente (MMA), 46 p.

BROCKERHOFF, E.G.; JACTEL, H.; PARROTTA, J.A.; QUINE, C.P.; SAYER, J. 2008. Plantation forests and biodiversity: oxymoron or opportunity? *Biodiversity and Conservation*, **17**(5):925-951. http://dx.doi.org/10.1007/s10531-008-9380-x

BRUM NETO, H.; BEZZI, M.L.; CASTANHO, R.B. 2007. Rio Grande do Sul: uma proposta de regionalização geoeconômica. *Sociedade & Natureza*, **19**:171-190.

CORDEIRO, J.L.P.; HASENACK, H. 2009. Cobertura vegetal atual do Rio Grande do Sul. *In:* V.D. PILLAR; S.C. MÜLLER; Z.M.S. CASTILHOS; A.V.A. JACQUES (org.), *Campos sulinos: conservação e uso sustentável da biodiversidade*.Brasília,Ministério do Meio Ambiente,p. 285-299.

DUARTE, L.S.; SANTOS, M.M.G.; HARTZ, S.M.; PILLAR, V.D. 2006. Role of nurse plants in Araucaria Forest expansion over grassland in southBrazil. *Austral Ecology*, **31**(4):520-528. http://dx.doi.org/10.1111/j.1442-9993.2006.01602.x

FISCHER, J.; LINDENMAYER, D.B. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography*, **16**(3):265-280. http://dx.doi.org/10.1111/j.1466-8238.2007.00287.x

FOCHT, T.; PILLAR, V.D. 2003. Spatial patterns and relations with site factors in a campos grassland under grazing. *Brazilian Journal of Biology*, **63**(3):423-436. http://dx.doi.org/10.1590/S1519-69842003000300008

FONSECA, C.R.; GANADE, G.; BALDISSERA, R.; BECKER, C.; BOELTER, C.R.; BRESCOVIT, A.D.; CAMPOS, L.M.; FLECK, T.; FONSECA, V.S.; HARTZ, S.M.; JONER, F.; KÄFFER, M.; LEAL-ZANCHET, A.M.; MARCELLI, M.P.; MESQUITA, A.S.; MONDIN, C.A.; PAZ, C.P.; PETRY, M.V.; PIOVENSAN, F.N.; PUTZKE, J.; STRANZ, A.; VERGARA, M.; VIEIRA, E.M. 2009. Towards an ecologically-sustainable forestry in the Atlantic Forest. *Biological Conservation*, **142**(6):1209-1219. http://dx.doi.org/10.1016/j.biocon.2009.02.017

FORTES, A.B. 1959. *Geografia física do Rio Grande do Sul*. Porto Alegre, Globo,393 p.

GAO, B.C. 1996. NDWI - A normalized difference water index for remote sensing ofvegetation liquid water from space. *Remote Sensing of Environment*, **58**(3):257-266. http://dx.doi.org/10.1016/S0034-4257(96)00067-3

GONÇALVES, E.T.; SOUZA, A.F. 2014. Floristic variation in ecotonal areas: Patterns, determinants and biogeographic origins of subtropical forests in South America. *Austral Ecology*, **39**(1):122-134. http://dx.doi.org/10.1111/aec.12051

GUADAGNIN, D.L.; ZALBA, S.M.; GÓRRIZ, B.C.; FONSECA, C.R.; NEBBIA, A.J.; CUEVAS, Y.A.; EMER, C.; GERMAIN, P.; WENDLAND, E.M.D.R.; PERELLO, L.F.C.; BASTOS, M.C.S.; VILLALOBOS, P.G. 2009. Árvores e arbustos exóticos invasores no Pampa: questões ecológicas, culturais e sócio-econômicas de um desafio crescente. *In:* V.D. PILLAR; S.C. MÜLLER; Z.M.S. CASTILHOS; A.V.A. JACQUES(org.), *Campos sulinos: conservação e uso sustentável da biodiversidade*. Brasília, Ministério do Meio Ambiente, p. 300-316.

GUSSO, A.; FORMAGGIO, A.R.; RIZZI, R.; ADAMI, M.; RUDORFF, B.F.T. 2012. SoybeancropareaestimationbyModis/Evi data. *Pesquisa Agropecuária Brasileira*, **47**(3):425-435. http://dx.doi.org/10.1590/S0100-204X2012000300015

HANSEN, M.C.; POTAPOV, P.V.; MOORE, R.; HANCHER, M.; TURUBANOVA, S.A.; TYUKAVINA, A.; THAU, D.; STEHMAN, S.V.; GOETZ, S.J.; LOVELAND, T.R.; KOMMAREDDY, A.; EGOROV, A.; CHINI, L.; JUSTICE, C.O.; TOWNSHEND, J.R.G. 2013. High-resolution global maps of 21st-century forest cover change. *Science*, **342**(6160):850-853. http://dx.doi.org/10.1126/science.1244693

HARDISKY, M.A.; KLEMAS, V.; SMART, M. 1983. The influence of soil salinity, growthform, and leaf moisture on spectral radiance of *Spartinaalterniflora* canopies.*Photogrammetric Engineering & Remote Sensing*, **16**:1581-1598.

HENDGES, E.R., PEREIRA, R.S.; ANDRES, J. 2012. Dinâmica das áreas de floresta nativa no Rio Grande do Sul no período de 1988 a 2020. *CiênciaFlorestal*, **42**:828-833.

HUNT, E.R.; ROCK, B.N.; NOBEL, P.S. 1987. Measurement of leaf relative water content by infrared reflectance. *Remote SensingofEnvironment*, **22**(3):429-435. http://dx.doi.org/10.1016/0034-4257(87)90094-0

KUINCHTNER, A.; BURIOL, G.A. 2001. Clima do estado do Rio Grande do Sul segundo a classificação climática de Köppen e Thornthwaite. *DisciplinarumScientia*, **2**:171-182.

MANTELLI, J. 2006. O setor agrário da região noroeste do Rio Grande do Sul Resumo Introdução. *Geosul*, **21**:87-105.

MATHER, P.M.; KOCH, M. 2011. *Computer Processing of Remotely-Sensed Images: An Introduction*, 4th ed., Oxford,Wiley-Blackwell, 462 p.

MCGARIGAL, K.; MARKS, B.J. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. United States Forest Service General Technical Report PNW-GTR-351. Corvallis, Oregon, USA.

METZGER, J.P.; DÉCAMPS, H. 1997. The structural connectivity threshold: an hypothesis in conservation biology at the landscape scale. *ActaEcologica*, **18**(1):1-12. http://dx.doi.org/10.1016/S1146-609X(97)80075-6

NAUMOV, A. 2005. Land Use in Brazil : Major Contemporary Changes and Their Driving Forces. *In:* E. MILANOVA; I. HIMIYAMA; Y. BICIK (org.), *Understanding land-use and land-cover change in global and regional context.* Enfield, Science Publishers, p. 207-223.

OLIVEIRA, J.M.; PILLAR, V.D. 2005. Vegetation dynamics on mosaics of Camposand Araucaria forest between 1974 and 1999 in Southern Brazil. *Community Ecology*, **5**(2):197-202. http://dx.doi.org/10.1556/ComEc.5.2004.2.8

OVERBECK, G.E.; MÜLLER, S.C.; PILLAR, V.D.; PFADENHAUER, J. 2006. Floristic composition, environmental variation and species distribution patterns in burned grassland in southern Brazil. *Brazilian Journal of Biology*, **66**(4):1073-1090. http://dx.doi.org/10.1590/S1519-69842006000600015

OVERBECK, G.E.; MÜLLER, S.C.; FIDELIS, A.; PFADENHAUER, J.; PILLAR, V.D.; BLANCO, C.C.; BOLDRINI, I.I.; BOTH, R.; FORNECK, E.D. 2007. Brazil's neglected biome: the south Brazilian campos. *Perspectives in Plant Ecology, Evolution and Systematics*, **9**(2):101-116. http://dx.doi.org/10.1016/j.ppees.2007.07.005

PEEL, M.C.; FINLAYSON, B.L.; MCMAHON, T.A. 2007. Updated world map of the Köppen-Geiger climate classification. *Hydrology and Earth System Sciences*, **11**(5):1633-1644. http://dx.doi.org/10.5194/hess-11-1633-2007

PINHEIRO, A.; LUIZA, R.; GRACIANO, G.; SEVERO, D.L. 2013. Tendência das séries temporais de precipitação da região sul do Brasil. *Revista Brasileira de Meteorologia*, **28**(3):281-290. http://dx.doi.org/10.1590/S0102-77862013000300005

QUADROS, F.L.F.; PILLAR, V.P. 2001. Dinâmica vegetacional em pastagem natural submetida a tratamentos de queima e pastejo. *Ciência Rural*, **31**(5):863-868. http://dx.doi.org/10.1590/S0103-84782001000500020

RIBEIRO, M.C.; METZGER, J.P.; MARTENSEN, A.C.; PONZONI, F.J.; HIROTA, M.M. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation*, **142**(6):1141-1153. http://dx.doi.org/10.1016/j.biocon.2009.02.021

RIITTERS, K.H.; O'NEILL, R.V.; HUNSAKER, C.T.; WICKHAM, J.D.; YANKEE, D.H.; TIMMINS, S.P.; JONES, K.B.; JACKSON, B.L. 1995. A factor analysis of landscape pattern and structure metrics.*Landscape Ecology,* **10**(1):23-39. http://dx.doi.org/10.1007/BF00158551

RIO GRANDE DO SUL. 2012. Atlas socioeconômico do Rio Grande do Sul -VAP da agropecuária. Available at: http://www.atlassocioeconomico.rs.gov.br. Accessed on: 10/08/2015.

RUDORFF, C.D.M.; RIZZI, R.; RUDORFF, B.F.T.; SUGAWARA, L.M.; VIEIRA, C.A.O. 2007. Spectral-temporal response surface of MO-

DIS sensor images for soybean area classification in Rio Grande do Sul State. *Ciência Rural*, **37**(1):118-125.
http://dx.doi.org/10.1590/S0103-84782007000100019

SCARIOT, E.C.; ALMEIDA, D.; EDUARDO, J. 2015. Connectivity dynamics of Araucaria forest and grassland surrounding Passo Fundo National. *Natureza & Conservação*, **13**(1):54-59.
http://dx.doi.org/10.1016/j.ncon.2015.05.001

SCHNEIDER, I. 1994. Êxodo, envelhecimento populacional e estratégias de sucessão na exploração agrícola. *Indicadores Econômicos FEE*, **21**:259-268.

SECRETARIA DA COORDENAÇÃO E PLANEJAMENTO (SPC). 2002. Atlas Socioeconômico do Rio Grande do Sul. 2nd ed.,Porto Alegre, SCP. Available at: http://www.scp.rs.gov.br/atlas/default.asp. Accessed on: 08/08/2015.

SOKAL, R.R.; ROHLF, F.J. 1995. *Biometry: The Principles and Practice of Statistics in Biological Research*. W.H. Freeman, New York, 937 p.

SOUZA, A.F.; CORTEZ, L.S.R.; LONGHI, S.J. 2012. Native forest management in subtropical South America: long-term effects of logging and multiple-use on forest structure and diversity. *Biodiversity and Conservation*, **21**(8):1953-1969.
http://dx.doi.org/10.1007/s10531-012-0287-1

SOUZA, A.F.; RAMOS, N.P.; PIZO, M.A.; HÜBEL, I.; CROSSETTI, L.O. 2013. Afforestation effects on vegetation structure and diversity of grasslands in southern Brazil: The first years. *Journal for Nature Conservation*, **21**(1):56-62.
http://dx.doi.org/10.1016/j.jnc.2012.10.002

SOUZA, I.F.S.; SOUZA, A.F.; PIZO, M.A.; GANADE, G. 2010. Using tree population size structures to assess the impacts of cattle grazing and eucalypts plantations in subtropical South America. *Biodiversity and Conservation*, **19**(6):1683-1698.
http://dx.doi.org/10.1007/s10531-010-9796-y

STRECK, E.V.; KÄMPF, N.; DALMOLIN, R.S.D.; KLANT, E.; NASCIMENTO, P.C.; SCHNEIDER, P.; GIASSON, E.; PINTO, L.F.S. 2008. *Solos do Rio Grande do Sul*. Porto Alegre, EMATER/RS, 222 p.

YUAN, J.; NIU, Z. 2008. Evaluation of atmospheric correction using FLAASH. *In*: First International Workshop on Earth Observation and Remote Sensing Applications (EORSA), Beijing, 2008.*Anais…* Beijing, **1**:1-6.

WILSON, H.E.; SADER, A.S. 2002. Detection of forest harvest type using multiple dates of Landsat TM imagery. *Remote Sensing of Environment*, **80**(3):385-396.
http://dx.doi.org/10.1016/S0034-4257(01)00318-2

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