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INTERPRETANDO PADRÕES ESPACIAIS DE HETEROGENEIDADE FUNCIONAL DE ECOSSISTEMAS NO RIO GRANDE DO SUL: UMA ABORDAGEM MEDIANTE USO DE IMAGENS MODIS-LAND

Marcela Pinillos Galindo

Tese apresentada ao Programa de Pós-Graduação em Ecologia da Universidade Federal do Rio Grande do Sul como um dos pré-requisitos para obtenção do título de Doutor em Ciências – ênfase em Ecologia.

Orientador: Prof. Dr. Valério DePatta Pillar

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Porto Alegre, dezembro de 2007.

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RESUMO

O conceito de 'ecossistema' emergiu da necessidade de compreender o caráter extremamente dinâmico da vegetação, interpretado a partir daí como o resultado da interação recíproca entre um dado complexo de organismos e seu conjunto amplo de fatores do ambiente físico. Um ramo das ciências ecológicas desenvolveu-se desse conceito, visando examinar o resultado de tais interações em termos de fluxos de energia, matéria e informação. Desenvolvimentos conceituais recentes apontam para uma concepção do ecossistema sob a ótica de um novo paradigma, para o qual aninhamento, hierarquia, decomposabilidade relativa, probabilidade e dependência de escala são critérios chave. Outro desenvolvimento importante, a análise de trajetórias, abriu a possibilidade de tratar a dinâmica e o funcionamento do ecossistema como fenômenos em múltiplas escalas.

Incertezas metodológicas e ecológicas decorrem numa visão pouco nítida de como o funcionamento e a estrutura do ecossistema interagem sob a influência de um determinado conjunto de fatores de uso e do ambiente físico. A situação demanda uma abordagem analítica na qual classificações funcionais e estruturais sejam implementadas independentemente, com o fim de estabelecer '*a posteriori*' quanto e como as classificações estão interconectadas. A tarefa é ainda mais desafiante, em termos de método e interpretação, quando consideramos o contexto hierárquico e complexo em que a análise deve ser feita e a dependência de definição dos resultados.

Esta tese refere-se ao desenvolvimento de ferramentas conceituais e metodológicas para analisar a heterogeneidade funcional dos ecossistemas no espaço, em relação a fatores significativos de uso e do ambiente, e aos diferentes tipos de vegetação presentes numa determinada região. Com esse objetivo, adotamos o conceito de 'Tipos Funcionais de Ecossistemas' (TFEs), os quais reúnem unidades espaciais com padrão de funcionamento similar, sem considerar seus atributos estruturais, e avançamos num esquema classificatório de TFEs que permite capturar as respostas funcionais de curto prazo dos ecossistemas em cenários de mudanças ambientais e de uso altamente dinâmicas. Também examinamos a sensibilidade dos tipos funcionais de ecossistemas a diferentes definições de funcionamento e parâmetros de escala espacial. Os TFEs provaram ser sensíveis a estas variáveis analíticas, oferecendo assim a possibilidade de indagar a natureza multidimensional e multi-escala dos fenômenos do ecossistema. Os TFEs capturam eficientemente os aspectos mais relevantes da resposta sazonal da vegetação aos fatores do ambiente biofísico, provendo assim uma ferramenta útil para descrever a heterogeneidade espacial do funcionamento dos ecossistemas em domínios temporais e geográficos específicos.

Nesta tese avançamos no reconhecimento e descrição dos principais tipos de paisagem no planalto basáltico do Rio Grande do Sul, e propomos mecanismos e controles responsáveis desses padrões característicos. Da associação espacial entre feições do terreno, solos, tipos de uso e vegetação, identificamos três tipos básicos de paisagens e definimos preliminarmente seu domínio espacial. Os resultados descrevem um forte relacionamento entre a distribuição dos grandes tipos fisionômicos de vegetação, os solos e os processos formadores de relevo. Assim sendo, os campos dominam onde relevo e solos indicam a ocorrência de remanescentes de uma antiga superfície de pediplanação, em quanto as florestas prevalecem onde os agentes geomorfológicos têm rejuvenescido a paisagem. Porém, com o objetivo de compreender os processos responsáveis destes padrões, é essencial fazer '*down-scaling*' desde a escala regional na qual os processos formadores de relevo e de solos dominam a diferenciação espacial de variáveis ecológicas, até a escala local na qual fatores biológicos e relacionados com o regime de distúrbio adquirem maior importância na produção de padrões de heterogeneidade espacial. Identificamos que a abordagem ecossistêmica funcional é a maneira mais promissora de relacionar processos de natureza tão divergente.

Palavras chave: tipos funcionais de ecossistemas, heterogeneidade funcional, MODIS NDVI, MODIS LAI, MODIS FPAR, paisagem, padrões espaciais.

ABSTRACT

The ‘ecosystem’ concept emerged from the need for understanding the highly dynamic nature of the vegetation, interpreted from thereon as the reciprocal interaction among the organism-complex and a wide array of factors of the physical environment. A full branch of the ecological sciences developed from this concept, aimed to assessing the outcome of such interactions as flows of energy, matter and information. Recent conceptual developments points to a conception of ecosystem as an entity evolving under the influence of a novel paradigm, for which nestedness, hierarchy, relative decomposability, probability and scale-dependency are central. Another important development, trajectory analysis, opens the possibility to treat ecosystem dynamics and ecosystem functioning as multi-scale phenomena.

Methodological and ecological uncertainties determine a rather fuzzy picture of how ecosystem function and structure interplay under the influence of some set of drivers of the physical environment and land use. The whole situation waits for an analytical path to be designed in which functional and structural classifications are carried out independently, in order to establish *a posteriori* whether they are connected and how they are connected. The task is even more defiant, both in terms of methods and interpretation, if we consider the already complex hierarchical context in which the analysis should be set and the definition-dependency of the outcome.

This thesis is about the development of conceptual and analytical tools for analyzing the functional heterogeneity of the ecosystems in the space, in relation to meaningful environmental and land-use factors and to the different types of vegetation present over a given region. To that aim, we adopt the concept of Ecosystem Functional Types (EFTs), which enclose spatial units with similar functional patterns, no attention paid to their structure, and advance on an EFT classificatory scheme that allows capturing the short-term functional response of the ecosystems to environmental and land-use changes. Furthermore, we examine the effect of using different surrogates of ecosystem functioning on the resulting picture of functional patchiness. The effect of changing parameters of spatial scale is also tested. The Ecosystem Functional Types proved to be heavily definition-dependent and sensitive to spatial scale, which allows exploring the multi-dimensional and multi-scale nature of ecosystem phenomena. The EFTs efficiently capture the most relevant features of the seasonal response of the vegetation to the drivers of the biophysical environment, providing so a useful tool for depicting the spatial heterogeneity of ecosystem functioning in a given geographic and temporal domain.

In this report we also accomplished the recognition and description of main landscape types in the basaltic tablelands of Rio Grande do Sul, and proposed mechanisms and controls responsible for their characteristic patterns. From the spatial association of terrain features, soils, land-use and vegetation, we identified three basic landscape types and broadly defined their spatial domain. The picture described tells of a rather close relationship among the distribution of the major physiognomic types of the vegetation, soils, land-use and land-forming processes. In this picture, the grasslands prevail where terrain and soil features suggest there are the remnants of an old pediplanation surface, while forests seems to dominate wherever geomorphic agents have rejuvenated the landscape. However, in order to understand the processes responsible of these patterns it is then essential to downscale from the regional realm where terrain and soil-forming phenomena dominate spatial differentiation, to the fine-scale processes at which biological and disturbance-related factors are most influential in the production of patterns of spatial heterogeneity. We identify the functional approach to the ecosystems as the most promising way to correlate processes of such a different nature.

Key words: ecosystem functional types, functional heterogeneity, MODIS NDVI, MODIS LAI, MODIS FPAR, landscape, spatial patterns.

Here hills and vales, the woodland and the plain,
Here earth and water seem to strive again,
Not chaos-like together crushed and bruised,
But, as the world, harmoniously confused:
Where order in variety we see,
And where, though all things differ, all agree.

ALEXANDER POPE (Windsor Forest, 1713)

INTRODUÇÃO GERAL

ORGANIZAÇÃO DA TESE

Esta tese foi organizada em forma de capítulos, seguidos por uma seção de considerações gerais em português. Os capítulos, separados em duas seções, constituem artigos independentes (com exceção do capítulo 2 que reúne dois artigos) elaborados e redigidos em língua inglesa, de forma a poder submetê-los com brevidade a revistas especializadas com circulação internacional. No início de cada capítulo, além do título, constam no rodapé os demais autores do trabalho. A formatação geral dos capítulos foi realizada uniformemente, conforme as orientações da revista **Ecosystems**, à qual submeteremos dois dos quatro artigos. As revistas às que se submeterão os artigos restantes ainda estão por definir.

INTRODUÇÃO AO CONTEÚDO

É um fato que, em todas as escalas espaciais, diferentes fontes de heterogeneidade ecológica dominam a relação entre vegetação e o ambiente (Weins 1989). Tal variabilidade, seja na forma de gradientes, mosaicos e/ou redes, determina assim mesmo a heterogeneidade dos fluxos de matéria, energia e informação dentro e entre os ecossistemas (White & Brown, 2005). Contudo a variabilidade espacial dos parâmetros funcionais que descrevem tais fluxos é complexa. Esta não responde de maneira linear e unívoca à distribuição dos parâmetros estruturais que definem tipos de vegetação, nem à heterogeneidade espacial das variáveis ambientais. A interpretação da variabilidade funcional no espaço é, no entanto, muito sensível a várias fontes de incertezas. Dessas destacamos as que emergem de limitações e inconsistências das metodologias empregadas, que determinam dificuldades na hora de extrapolar os dados no espaço e compará-los, as que resultam da forma como os fatores envolvidos são definidos e descritos e as que decorrem da não linearidade mesma da trama de relações ecológicas. Embora a tarefa de indagar as causas por trás da heterogeneidade funcional seja difícil, resulta cada vez mais claro que tal heterogeneidade é de extrema importância para interpretar e predizer a dinâmica espaço-temporal dentro e entre os ecossistemas (White & Brown 2005, Turner & Chapin 2005)

O presente trabalho tem como principal objetivo o desenvolvimento de ferramentas conceituais e metodológicas para analisar a heterogeneidade funcional de ecossistemas. Visamos a interpretação, numa área da região sul do Brasil, da diversidade de tipos de vegetação e da variabilidade dos fatores ambientais em termos da produção de padrões de heterogeneidade funcional. A heterogeneidade funcional, no entanto, é descrita na forma de mapas categóricos cujas unidades são definidas sobre a base de padrões comuns de variação sazonal de parâmetros funcionais. Entidades espaciais definidas exclusivamente sobre a base desses padrões sazonais são chamadas 'Tipos funcionais de ecossistemas' (ou TFEs: ver Paruelo et. al. 2001, Alcaraz et. al. 2005)

O trabalho consta de duas seções, cada seção dividida em dois capítulos. A primeira seção fornece o embasamento teórico e ecológico-regional que permite, nos capítulos da seção subseqüente, discutir de maneira aprofundada o significado ecológico dos TFEs. Nesta primeira seção, começamos com um ensaio que trata aspectos teóricos, no contexto da ecologia de ecossistemas, da interação entre vegetação e ambiente na produção de padrões espaciais de heterogeneidade funcional. Com uma visão histórica da evolução operativa do conceito de ecossistema identificamos as diversas fontes de incerteza que desafiam a descrição, a análise e a interpretação satisfatória desses padrões. Discutimos algumas maneiras inovadoras de abordar a problemática, dando especial ênfase ao conceito de Tipos Funcionais de Ecossistemas, avaliando criticamente a maneira como esses tipos foram inicialmente definidos por Paruelo *et al.* (2001) e propondo critérios alternativos de definição de maneira a torná-los mais sensíveis às mudanças de curto prazo nos padrões de clima e uso da terra. Continuamos com uma revisão dos dados disponíveis para a identificação dos TFEs e concluímos sobre a contribuição potencial deste tipo de classificações à compreensão e à modelagem multi-escala das relações funcionais entre cobertura vegetal e fatores do ambiente.

No segundo capítulo apresentamos o contexto ecológico regional da área de estudo, localizada na porção norte do estado de Rio Grande do Sul. Nesta região a feição topográfica dominante é o extenso planalto modelado sobre material extrusivo do Mesozóico, sendo que processos associados ao soerguimento do planalto durante o Cenozóico determinaram distribuição e características das principais unidades geomorfológicas da área. Do ponto de vista da vegetação, a ocorrência generalizada de mosaicos de floresta e campo confere à região uma fisionomia característica. Porém, as causas que explicam os mosaicos ainda são objeto de discussão (ver Pillar 2003, Duarte et al. 2006 e referências ali listadas). O fim deste capítulo é o enquadramento da problemática ampla da heterogeneidade funcional no contexto de um problema ecológico específico, neste caso a coexistência de ecossistemas contrastantes (campos e florestas) em uma região relativamente homogênea do ponto de vista de clima e geologia. Tal enquadramento visa clarificar como o enfoque funcional dos TFEs pode subsidiar a compreensão dos processos responsáveis pela formação de padrões espaço-temporais de vegetação e ecossistemas. Igualmente, esta análise contribui na identificação dos fatores ambientais relevantes para a interpretação da heterogeneidade funcional.

As principais perguntas a serem respondidas neste trabalho são: 1- Como são os padrões de distribuição da vegetação que dominam na região? 2- Como estão esses padrões relacionados com os fatores regionais de diferenciação do ambiente físico (tectônica, clima, geomorfologia e processos de formação de solos)? 3- Como esses fatores, que atuam na escala regional, modulam na escala local os processos responsáveis do *turn-over* espacial de ecossistemas? 4- Como interagem os processos específicos das diferentes escalas espaciais na produção dos padrões observados?

Uma revisão critica de literatura sobre os processos do ambiente físico e da história de uso, conducentes esses à segregação espacial dos grandes tipos regionais de paisagem, é acompanhada de reconhecimento de campo (5 campanhas realizadas desde março de 2004 até novembro de 2005), interpretação visual e classificação de imagens LANDSAT TM (compostas falsa-cor, bandas 5, 4 e 3, junho a outubro 2001, escala 1: 250.000) e SRTM (escala aprox. 1: 100.000). Identificamos unidades regionais de paisagem sobre a base de topografia, vegetação e uso. Dentro dessas unidades selecionamos áreas de aproximadamente 56 Km^2 para analisar padrões de distribuição de usos e tipos de vegetação em relação às formas de terreno e tipos de solo. Concluímos sobre a associação espacial dos diferentes componentes da paisagem (unidades de vegetação/uso, unidades de solo, formas de relevo), avançamos hipóteses que expliquem tal associação e discutimos a contribuição potencial do enfoque funcional dos TFEs na avaliação das hipóteses apresentadas.

A segunda seção do trabalho trata especificamente da classificação da área de estudo em unidades funcionalmente homogêneas (TFEs), sobre a base de imagens MODIS *Spectral Vegetation Indices* (MOD13) e LAI/FPAR (MOD15). Com o fim de diminuir fontes de incerteza na interpretação das unidades funcionais, da área analisada previamente (segundo capítulo da primeira seção) selecionamos uma área menor, a qual foi mais intensamente reconhecida e registrada durante as campanhas de trabalho de campo. Imagens MODIS correspondentes ao ciclo anual de 2002 foram escolhidas para determinar a heterogeneidade funcional do período correspondente. Os principais objetivos desta segunda seção são os de: 1- definir uma metodologia robusta de classificação de TFEs, 2- avaliar a associação espacial das unidades funcionais com unidades definidas a partir de variáveis estruturais da vegetação ou fatores ambientais, 3- determinar a sensibilidade do método classificatório à forma como a área de estudo é descrita funcionalmente. No entanto, essa descrição funcional varia em relação a três componentes, o primeiro dos quais se refere à natureza das variáveis a partir das quais descrevemos o funcionamento do ecossistema (dependência de definição da heterogeneidade funcional), e os outros dois à escala espaço-temporal na qual circunscrevemos o funcionamento. Porém, o nosso método fixa os parâmetros de escala temporal, de maneira que todas as classificações de TFEs empregam um mesmo intervalo de tempo e similar comprimento das séries de tempo. No entanto, o estudo de variações devidas ao uso de diferentes ciclos anuais corresponderia a uma fase mais avançada da análise e portanto ainda não foram avaliados. É assim que só a natureza das variáveis funcionais e os parâmetros que definem o seu domínio espacial são relevantes como fontes de variação de nossos resultados.

No primeiro capitulo desta segunda seção (Capítulo 3) desenvolvemos um método de classificação de Tipos Funcionais de Ecossistemas, baseado na identificação de trajetórias sazonais de descritores de funcionamento selecionados. Esses descritores são definidos sobre a base do seu significado ecológico e alta variabilidade espacial, e calculados a partir de séries temporais de imagens MODIS (MOD13 e MOD15). Como um simples ciclo anual é considerado, a classificação funcional pode resultar muito sensível às variações aleatórias de clima o de fatores biológicos, razão pela qual foi necessário avaliar quanto os TFEs realmente descrevem padrões ecologicamente significativos de variabilidade funcional. Os TFEs, portanto, foram avaliados em termos do seu ajuste a alguns enunciados chave: 1- o funcionamento dos ecossistemas é um atributo multidimensional da vegetação em relação ao seu ambiente. 2- esse funcionamento pode ser descrito de múltiplas maneiras, porém decorre da natureza interligada dos processos funcionais no ecossistema que o zoneamento funcional resultante de uma dada definição deve estar espacialmente associado a qualquer outro zoneamento resultante de uma definição diferente. 3- Assim mesmo, qualquer uma que for a definição de funcionamento a partir da qual a heterogeneidade é descrita, deve se manter que a classificação de TFEs responde sensivelmente aos padrões de distribuição da fisionomia da vegetação, do uso da terra e de outros controles ambientais. A partir dos resultados obtidos discutimos a influencia da definição de funcionamento sobre a estrutura da classificação funcional e sua associação espacial com a distribuição de tipos de vegetação e unidades ambientais. Baseamos essa discussão num esquema analítico vindo da Teoria da Informação no qual a informação, contida em tabelas de contingência bi e tridimensionais, é interpretada em termos de diferentes tipos de interação e associação entre as categorias das diferentes classificações (Orlóci et al. 2002). Tabelas bidimensionais são as que contêm a freqüência de pixels das classes funcionais derivadas da série temporal MOD13 dentro das classes da classificação derivada da série temporal MOD15. Assim mesmo, tabelas tridimensionais são as que contêm a freqüência de pixels de uma classificação de TFEs dentro das categorias da classificação ambiental (unidades de solo) e dentro dos tipos de vegetação (classificação fisionômica e de uso). Finalmente, analisamos como a relação, entre unidades funcionais e fisionômicas da vegetação, depende do contexto ambiental, ou seja, varia de um tipo de solo para o outro e pode determinar divergências funcionais dentro de um determinado tipo fisionômico e/ou convergências funcionais entre tipos fisionômicos diferentes.

O último capítulo da tese (segundo capítulo da segunda seção ou Capítulo 4) trata do problema da mudança nos parâmetros de escala espacial na definição e arranjo das categorias de heterogeneidade funcional. Em relação às imagens obtidas por sensoriamento remoto, a escala espacial é definida segundo King (2005) como a caracterização física da dimensão espacial da área coberta por uma dada imagem ou série temporal de imagens (conjunto de dados geo-referenciados). Tal caracterização toma a forma de dois parâmetros: extensão e tamanho de pixel. Um parâmetro adicional, locação, determina o domínio geográfico e ecológico das imagens. Neste capítulo, enquadramos nossa problemática no que na literatura tem se chamado o “problema da unidade de área modificável” (MAUP: Jelinski & Wu 1996), o qual tem maior importância quando lidamos com fenômenos multi-escala, como é o caso do funcionamento ecossistêmico. O MAUP trata da variação potencial dos resultados da análise de um conjunto de dados geo-referenciados, quando essa variação é decorrente de mudanças nas dimensões do conjunto e/ou na definição das unidades do conjunto. Além da sensibilidade da classificação funcional ao MAUP, avaliamos o efeito de modificar a representação relativa das unidades de vegetação e tipos ambientais, isto é o domínio ecológico da área para a qual descrevemos a heterogeneidade funcional, assumindo que o efeito da mudança nos parâmetros de escala não é independente da configuração da paisagem.

Com estes objetivos, classificamos TFEs para a área de estudo a partir de dados de NDVI vindos de imagens MODIS SVI (MOD13) correspondentes ao ciclo anual de 2002. As séries temporais empregadas têm resoluções de 62.5 x 10^3 m^2 e 1000 x 10^3 m^2, o que permitiu avaliar a sensibilidade do método classificatório ao tamanho de pixel. Igualmente, escolhemos três subáreas de diferente extensão dentro da área de estudo, isolamos os dados correspondentes e identificamos os TFEs em cada uma delas a partir dos dados isolados. Ao compararmos os resultados de cada subárea com os da sua porção correspondente na classificação geral, avaliamos a sensibilidade do método à mudança de extensão espacial dos dados geo-referenciados. Igualmente, ao compararmos o efeito de cada parâmetro, isoladamente e em relação ao outro, entre as subáreas, estamos também apreciando a influência das diferentes configurações paisagísticas no efeito dos parâmetros de escala. Sobre a base destes resultados avançamos conclusões sobre como a estrutura quantitativa e o arranjo de entidades funcionais responde às dimensões espaciais (resolução e extensão) das bases de dados NDVI, porém de maneira complexa e em relação à heterogeneidade ambiental e vegetacional da região.

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SECTION 1

THE ANALYTICAL SCENARIO OF ECOSYSTEM FUNCTIONAL TYPES: CONCEPTS, DATA AND ENVIRONMENTAL SETTING

Chapter 1. Ecosystem functional types, a functional approach for scaling the interaction between the vegetation and its environment

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TANSLEY'S HERITAGE: THE ECOSYSTEM FRAMEWORK

When A.G. Tansley (1935) wrote his famous 'The use and abuse of vegetational concepts and terms', he devoted the very first phrase to stress that "… the vegetation is constantly undergoing various kinds of change…". Tansley was certainly under the influence of several remarkable thinkers of the late 19th century, such as Kerner Von Merilaun and Vasily V. Dokuchaiev, whose views gave foundation to the ecological science. Von Merilaun (Conrad 1951) was the first to notice the dynamic nature of the vegetation by declaring that '*plant communities are developmentally connected in time through compositional changes*'. He also came to see basic regularities in the distribution of plant communities along topographic gradients, each community occurring on specific soils and associated environmental conditions. Two decades later, Dokuchaiev (Boulaine 1984) produced the first comprehensive theory of soil development by declaring that the spatial distribution of the soils was due to the interaction, throughout time, of four biophysical factors: parent material, climate, geomorphic processes and organisms.

According to Anker (2002) the 'ecosystem' concept emerged from what Tansley saw as the need for understanding the highly dynamic nature of the vegetation, dynamics that to that date had been largely imputed to biological interactions within 'supra-organismal', self-regulated ecological entities. Tansley rejected such a stance and ascribed ecosystems existence and dynamics to the reciprocal interaction among the organism-complex and a wide array of factors of the physical environment, in a similar manner as Dokuchaiev had done with the factors responsible of soil formation and evolution. From that point on, the physical factors of the environment were no more mere external forcings acting upon the ecological entities, but integral components of the entities them-selves (Shugart 1988).

During the following decades, a full branch of the ecological sciences developed from the ecosystem, aimed to assessing the outcome of such interactions as flows of energy, matter and information (White & Brown 2005). That such had been the chosen goal of ecosystem ecology certainly reflected major scientific breakthroughs of that time, in the thermodynamics and biogeochemistry fields (Golley 1991), and ensued what Tansley had marked as most relevant of the systemic nature of these ecological entities: the restless interchange of the most various kinds among their living and non-living components. Outstanding moments of this evolution were the work of Raymond Lindeman (1942) on the trophic-dynamics of a lake in Minnesota, H.T. Odum's (1953) 'Fundamentals of Ecology' and B.C. Patten's (1959) cybernetic interpretation of Lindeman's work.

It has been clear, all along the historical ascent of the ecosystem science, that its functional core poses important methodological challenges. Aimed to compose a *motion-picture* of the interaction between some defined complex of organisms and their non-living environment, ecosystem ecology advances by the sequential comparison of *static-pictures* of some selected components; flows have then to be inferred from the differences between successive pictures (see Sala & Austin 2000, Lauenroth 2000 and references therein). Nevertheless, obtaining a single picture can be a very difficult task, since the quantification of some ecosystem components or parameters frequently defies the technology available, comprises several sources of uncertainty and/or implies a huge effort in the field. The potential magnitude of the challenge was clear from the very beginning, as well as some of the necessary shortcuts. In his seminal paper, right after defining the 'ecosystem', Tansley stated that ecological entities should be isolated for purposes of study, notwithstanding that isolation is partly artificial. Likewise, when their boundaries, properties and composition are defined, ecosystems are always simplified to a variable degree in order to make them methodologically accessible and comprehensible with the theoretical elements at hand. Isolation and simplification both call for homogeneity: homogeneous habitat factors setting the spatio-temporal extent of so-defined ecosystems, the *ecotope* after Tansley, and homogeneous components and interactions giving them some 'typical' physiognomy (see, for instance, Box 1981) and/or functional identity. Such isolation have allowed to generalize functional information, as collected in 'representative' experimental plots, to the complete 'ecologically homogeneous' area from which the plots were drawn.

It is a fact that different sources of heterogeneity rule ecosystem processes at every possible spatial scale, forming gradients, patches or networks of variation (White and Brown 2005). Cases abound in which within-system spatial variability is higher than that between different types of ecosystems, as it has been observed among tropical rainforests when their aboveground biomasses are compared (Sarmiento *et al.*. 2005). Nevertheless, ecosystems are largely held as being spatially homogeneous in terms of their associated drivers of the physical environment, as well as in terms of the structural and functional traits of their characteristic vegetation. The inevitable variation has been mostly dealt with as if it were caused by the reign of chance. The handling of temporal variability, those various kinds of change that are constantly undergone by vegetation, as observed by Tansley, is the prime object to science's inquiry. Yet, simplification has been possible in these too by assuming a universal tendency towards a single state of dynamic equilibrium. Temporal variations of ecosystem functional traits have been then largely interpreted as corresponding to different phases of the system's transition through a successional ladder, towards a predictable climax stage. This notwithstanding, novel concepts such as scale dependence of perception of stability, attractor migration, alternating process phases dominated by determinism or randomness, occlusion, turbulence (non-linearity) and the likes have also been operational terms and concepts when it comes to suggesting general tendencies of vegetation dynamics at any time scale (Orlóci 2001). Yet the lacking of sufficient, comparable and temporally representative data describing the function of the ecosystems has hampered to a great degree the application of these novel concepts to the temporal dynamics of ecosystem functioning.

The conceptual model behind spatio-temporal simplifications is one of a direct relationship between ecosystem structure and function, in which to a given set of habitat factors corresponds a unique type of vegetation. In spite of the debate on which would be the most suitable traits to typify the vegetation (see Orlóci 1991, Chapin 1993 and references therein for overviews on the subject), there was general agreement that a single representative pattern of matter, energy and information exchange would arise from a given vegetation in a given environmental context. It is worth to mention that this model worked acceptably well for many years and was particularly successful to organize an increasing body of knowledge at planetary and continental scales (Golley 1991). Under its influence, comparative ecosystem ecology provided a robust tool to identify those drivers of the physical environment which are setting the geographical extent of global and regional ecosystems, including their main structural and functional features. Results of the efforts can be seen in Sarmiento (1984), Lieth and Verger (1992) and Coupland (1993), among others. Likewise, a vast net of experimental plots was established, in the context of the International Biological Program (Smith 1968), to provide valuable information on the rates of key processes related to the carbon, water and nutrient budgets of chosen global ecosystems. Some of these plots, plus others added during recent years, continue operationally in the context of the worldwide network of Long Term Ecological Research (LTER) sites (http://www.lternet.edu/).

Although these achievements certainly are a major gain in our understanding of ecological phenomena, and all of them were possible thanks to a rather simple conceptualization of the ecosystems, they led ecologists to face increasing degrees of functional and structural complexity which claimed for a more complex realization of the ecosystems. The theoretical foundations of the ecosystem concept have been questioned in the processes. Ulanowicz (1999) uncovered the Newtonian stance that still dominates the ecosystem science and questioned its ability to prescribe our observations of the living world. O'Neal (2001) emphasized what he saw as the irreconcilable essence of the systemic, mechanistic approach with the metastable, far from equilibrium and adaptive nature of ecological reality. The outcome points to a conception of ecosystem as an entity evolving under the influence of a novel paradigm, for which nestedness, hierarchy, relative decomposability, probability and scale-dependency are central (Wu 1995). Another important development, trajectory analysis, opens the possibility to treat ecosystem dynamics as a multi-scale phenomenon, replacing the idea of the equilibrium state with the ever migrating dynamic attractor in a very pragmatic and from the point of data analysis, very operational conceptual package (Orlóci et al. 2002, 2006). Concerning the relation among structure, function and environmental drivers, this changing conceptual scenario raises deep questions and offers exciting new possibilities.

ECOSYSTEMS AND ECOSYSTEM FUNCTIONAL TYPES

Some degree of isolation and simplification keeps being a distinguishing mark of scientific endeavors; therefore, so it is the expectation of a certain degree of homogeneity. However, as the theory advance towards more complex models of reality, the conceptual elements on which we base isolation and simplification also change. In the case of the ecosystem science, it is now accepted that variability has to be faced accordingly to its critical influence on ecosystem dynamics (White & Brown 2005, Turner & Chapin 2005). One of the new approaches is the hierarchical patch dynamics (HPD) framework, which deals with the subject by redefining variability, either environmental, functional or structural, as a nested hierarchy of mosaics. Mosaic cells (homogeneous domains), at each level of the hierarchy, would emerge from the *nearly-decomposable* nature of ecological entities (Wu 1995, Burnett & Blaschke 2003) and the chosen criteria to set apart homogeneous domains would be always dependent on scale, hierarchical level and problem definition.

The HPD approach surely is a more sophisticated and reliable framework to account for variability; however, it leaves unchallenged the univocal and simple relation proposed for function and structure (see Wu, 1995 and 1999). If asked about the correspondence of a nested mosaic defined by structural attributes, when compared with some functionally-defined arrangement, one would anticipate a high degree of redundancy and spatial overlap of variation patterns. The ecosystem theory, according to which there exists a reciprocal connection between ecosystem structure and function, seems to prescribe that. Nevertheless, many ecosystem ecologists believe that such may not be the case.

Milchunas and Lauenroth (1995) found that, several years after cessation of a fertilization and irrigation experiment, short grass steppe was experiencing structural changes that had not been evident soon after the experiment was finished; changes were consistently different among parcels subjected to different treatments and not related to subsequent climatic changes. Although functioning had readily responded, as revealed by litter accumulation, structural parameters (i.e. species composition) fell behind to respond and to recover from the experiment. In a similar manner, a fertilization experiment, conducted on a track of hyper seasonal tropical savannas during the growing seasons of 1997 and 1998 (Sarmiento *et al.*. 2006), evidenced a noticeable functional response (increased aboveground primary productivity) to the nutrient flush, but the relative share of aboveground biomass by the dominant grasses remained stable throughout. These results, which suggest that the structure of an ecosystem may be more conservative than its functional patterns when the system faces disturbance or sustained environmental change, question the assumed linearity of the relation between function and structure.

Likewise, Paruelo *et al.*. (2001) found an ambiguous correspondence between functionally- and structurally-defined areas in temperate South America. They classified the entire region according to some seasonal traits of the Normalized Difference Vegetation Index (NDVI), to obtain the geographical distribution of areas with similar pattern of carbon and energy exchange. The functional classification was then contrasted against a map of plant-cover types, for which the typification criterion had been structural (physiognomy as derived from phytogeographic units and land-use). From the 19 functional units set apart, just one revealed a 100 per cent coverage of a single structural unit, while only for other six the correspondence was higher than 90 per cent. None of the structural units were completely covered by a single functional class. When the analysis was repeated for the Iberian Peninsula (Alcaraz *et al.*. 2006), again a broad, instead of a clear-cut, correspondence between functional and structural units was found. In these cases, besides the complexities of the interaction between the two aspects of the ecosystems, also intervened uncertainties due to the method: different classification procedures and sources of data, most likely obtained at different spatial resolutions, were used to describe the vegetation by its physiognomy and by its functional traits.

In the scenario drawn so far, it should be mentioned that vegetation structure and ecosystem function are multi-dimensional concepts for which it is not any ‘evident’ way to describe them in order to enhance their reciprocal correspondence (Pillar & Orlóci 1993, Diaz & Cabido 1997, Smith *et al.*. 1997, Pillar 1999, Kleyer 2002 and references therein). Moreover, even though it is frequently implicit in the related literature that classification schemes based on the vegetation adaptive traits are related to the factors shaping ecosystem functional patterns, some authors have noticed the lack of robust empirical support (see Walker *et al*. 1999). Pillar & Sosinski (2003) suggested that any structural description of the ecosystems should take into account within-species variability, that is species plasticity, in order to reveal structural changes associated to short-term functional responses that are not evident when the basic unit is the species. However, plastic variations within the populations of the dominant species may not necessarily lead to sustained structural changes at the ecosystem level.

Being so, methodological and ecological uncertainties would most likely derive a rather fuzzy picture of how ecosystem function and structure interplay under the influence of some set of drivers of the physical environment and land use (habitat factors in the widest sense, according to Tansley). The whole situation waits for an analytical path to be designed in which functional and structural classifications are carried out independently, in order to establish *a posteriori* whether they are connected and how they are connected. The subsequent step would be checking which habitat factors actually influence their relationship. As crispy outcome is not to be expected, ecosystem science should certainly account for situations in which, within a given set of functional units, structurally different types of vegetation are included, each one having a certain probability. Finding how these probabilities are distributed in a phase-space determined by meaningful habitat factors, should render a most insightful picture of the ecosystem phenomena. The task is even more defiant, both in terms of methods and interpretation, if we consider the already complex hierarchical context in which the analysis should be set and the definition-dependency of the outcome: different functional properties will most likely render dissimilar functional classifications, differing probability functions for structural units, and so on.

The concept of Ecosystem Functional Types (EFT) is an advance in this direction; it was proposed by Paruelo *et al.*. (2001) to enclose spatial units with similar functional patterns, no attention paid to their structure (i.e. species, life forms or plant functional types composition). EFTs are conceptually related to plant functional types (PFTs), but are defined at a different level of organization: While EFTs refer to different aspects of the ecosystem matter and energy exchange, PFTs collect plants which are typed according to some set of characters with functional meaning, unconstrained by phylogeny (Chapin 1993) or any external species-based taxonomy (Orlóci 1991, Pillar & Orlóci 1993, Pillar 1999). Functional meaning at the plant level may refer to adaptability, regarding the environment, as it follows from Pillar and Orlóci (1993, (*response types* according to Walker 1997), to plant attributes in relation to some ecosystem function (*effect types*), to process-drivers such as the leaf C:N ratio, plant size or specific leaf area, in connection with the system carbon budget (see Walker & Langridge 2002, Lavorel & Garnier 2002), or to other characters such as those related to plant effects on herbivory (Blanco *et al.* 2007). At the EFTs level, functional traits should serve as descriptors of the *temporal patterns of some ecosystem process* (from hereon, ecosystem functioning) and are derived from temporal series of remote-sensing data (Paruelo *et al.*. 2001, Alcaraz *et al.*. 2006). The fact EFTs and PFTs are defined at different organization levels allow us to use them as complementary elements of the same analysis, in which the interaction between function and structure is assessed in terms of the spatial association of the EFTs with the frequency of *patches of PFTs* (after Bonan *et al.*. 2002). In such a case, the structural characterization of the ecosystem functional types could be given in terms of their composition of PFTs homogeneous domains.

SOURCE DATA FOR FUNCTIONAL CLASSIFICATIONS

Remote sensing and ecosystem functioning

To classify a given region into functionally homogeneous units, suitable data with total coverage, uniform resolution and temporal representativeness are needed. Only remote sensing can provide this kind of information. Remote sensing techniques include many active and passive tools of data acquisition, from which the most widely used are the optical multi-spectral scanners. These measure the brightness or the reflectance of sun-illuminated surfaces at defined wavelengths (Running *et al.*. 2000). These reflectance values are then used to derive a wide array of measures of the vegetation activity such as the several spectral vegetation indices: the Normalized Difference Vegetation Index (NDVI), the Enhanced Vegetation Index (EVI), the Land Surface Water Index (LSWI) or the Soil Adjusted Vegetation Index (SAVI, Broge & Leblanc 2000). Running *et al.* (2000) presented a brief, yet comprehensive overview on the theoretical background and methods used for estimating gross and net primary production from NASA-EOS satellite imagery. According to them, the most used spectral vegetation index, NDVI, which uses the reflectances from red and near-infrared wavelengths, is appropriate to compute the amount of photosynthetically active radiation actually absorbed by the vegetation cover. This amount might be multiplied by an empirical, ecosystem-dependent parameter, ε, to convert the energy absorbed into values of daily net photosynthesis. Other spectral vegetation indices, like EVI, use more than two spectral bands and seems particularly useful under conditions of high aboveground biomass or aerosol-polluted atmosphere, where the NDVI curves get saturated or underestimates vegetation activity (Huete *et al.*. 2002).

At the moment, two types of calibrated temporal series of vegetation indices, differing in terms of resolution, time covered and time step, are available worldwide: Pathfinder-derived AVHRR and MODIS datasets. Whereas AVHRR temporal series have proven suitable for analysis at a global scale, as a consequence of its coarse resolution, and cover on a temporal extent of almost 30 years, moderate-resolution MODIS datasets appear to be more appropriate for regional studies of ecosystem functioning and dynamics though its temporal coverage is still short (it was launched in 1999). MODIS improved hyperspectral, multi-angle sensor was launched in satellites (Terra and Aqua) with more stable orbits. The MODIS data processing is based on better algorithms to account for atmospheric uncertainties. These features altogether would render more reliable information on vegetation activity (Justice *et al.*. 1998). MODIS time-series are compounded by level 3, (temporal and spatial composite indices), and level 4 (modeled parameter) images from the Earth Observing Data Information System. Because they are obtained synergetically from a common set of reflectance records and because they represent interconnected processes, MODIS indices and functional parameters exhibit both redundancy and complementarity, that make them suitable for exploring ecosystem functioning in the sense of differentiating units with divergent functional attributes, as well as for emphasizing common patterns in classifications obtained from dissimilar indices and/or parameters.

MODIS functional parameters

The Moderate Resolution Imaging Spectroradiometer (MODIS) is an EOS (Earth Observing System) facility instrument designed to measure biological and physical processes on a global basis, every two to three days. According to Parkinson and Greenstone (2000) it employs a conventional imaging-radiometer concept, which consists of a cross-track scan mirror, but the assembly is double-sided and continuously-rotating. The optical arrangement provides imagery in 36 discrete bands from 0.4 to 14.5 μm, selected for diagnostic significance in Earth science. Two spectral bands have spatial resolutions of 250m at nadir, while five and 29 bands have resolutions of 500 and 1000m respectively, signal-to-noise ratios are greater than 500 at 1-km resolution (at a solar zenith angle of 70°); and absolute irradiance accuracies are ±5 percent from 0.4 to 3 μm (2 percent relative to the Sun) and 1 percent or better in the thermal infrared (3 to

14.5 μm). MODIS instruments provide daylight reflection and day/night emission spectral imaging of any point of the Earth.

Friedl *et al.* (1995) ascribe uncertainty production and propagation, for data retrieved by remote sensing, to the interaction of electromagnetic radiation, sensor devices, land surfaces and the atmosphere. Although well-defined functional relationships between remotely sensed data and key land-surface biophysical parameters would allow estimating biophysical parameters from remote sensing (data inversion), uncertainties render this task operationally arduous and question the stabiity of its outcome. Strahler *et al.* (1986) broadly defined three components for the data acquisition process: a scene component, a sensor component and an atmospheric component. The scene accounts for topographic, land-cover and ecological influences on surface radiances. The sensor component determines the number of bands recorded and their wavelength intervals, resolution, orbital aspects, scanner angle, instantaneous field of view and sensor technical degradation throughout time. Likewise, the atmospheric component takes into consideration atmospheric path radiance and absorption specific for every wavelength. In the case of the MODIS project, uncertainty sources of each data-acquisition component have been brought under more careful control.

Counts of the 36 MODIS channels are used for geolocation, calibration and processing. Quality indicators are added to the data to register missing or bad pixels and instrument modes. This fact, along with the MODIS instrument on-board auto-calibration capacity, reduces to great extent data uncertainties arising from sensor technical problems (Parkinson & Greenstone 2000). Geolocated and calibrated data are then converted into surface reflectance measures, which are given as if they had been measured at the surface of the Earth. To achieve so, sensor counts enter a very complex atmospheric-correction routine that models the effect of different sun-target-sensor geometries, under given scenarios of atmospheric composition. That is possible thanks to the many bands recorded and their variable sensitivity to relevant physical-chemical conditions of the atmosphere: some bands are used to estimate atmospheric water-vapor, aerosols and other influences on upwelling reflectances. Furthermore, increased sensor resolution and thinner bands diminishes off-nadir and scale-dependent data degradation (Friedl *et al.*. 1995, Huete *et al.*. 1999), reduces spectral vegetation indices saturation and enhances band sensitivity to important ecological processes (Justice *et al.*. 1998, Huete *et al.*. 2002). Equally relevant is the worldwide effort to validate MODIS data and outputs of data inversion. The measures of product accuracy and uncertainty are generally based on comparisons with in-situ data, data and products from other air- and space-borne sensors, and analyses of seasonal and inter-annual trends in the MODIS products. A network of core validation sites forms the basis of MODIS land validation activities, forming a system for regionally and globally extensive measurements and comparisons (see, for instance, Tian *et al.*. 2002b, Shabanov *et al.*. 2003, Engel-Cox *et al.*. 2004, Tan *et al.*. 2005). Influences of the scene-component characteristics on data, such as within-pixel ecological heterogeneity, are also disclosed through validation activities. In Figure 1, we present an overview of MODIS data-processing architecture and products. In summary, technical and conceptual improvements, in a context of active scientific validation, make of MODIS products (we refer in particular to those of the Land discipline: see Table 1) much better sources of information on the functioning of terrestrial ecosystems, than any other dataset previously available.

In spite of these advantages, it seems that some MODIS-Land products are not suitable for the classification of Ecosystem Functional Types. From the datasets listed in the table, MOD11, MOD14 and MOD43 are not directly related to vegetation functioning and dynamics, though MOD11 and MOD43 serve to yield related products. MOD12 dataset is already the outcome of a classification, in which some features of the plant-cover spectral response are used to prescribe some structurally-defined types of vegetation (Strahler *et al.* 1999, Lotsch *et al.* 2003). Likewise, MOD44 is a structural interpretation of the plant-cover phenology, whose reliability is still to be assessed in large areas of the world. Neither MOD12 nor MOD44 datasets are suitable for describing ecosystem functioning and their outcomes present variable proportions of misclassified pixels in areas where validation sites are absent. From the MOD17 products, NPP datasets lack the temporal resolution needed to depict seasonal patterns of matter and energy exchange, but the NPS datasets, on the other hand, would serve functional classification purposes if their results were not as heavily distorted as they are by the coarser resolution of the climatic data used to run the corresponding algorithm (for further information see Running *et al.* 1999). Therefore, just two MODIS-Land products seem appropriate to classify Ecosystem Functional Types: MOD13 (spectral vegetation indices) and MOD15 (LAI / FPAR).

MOD13 spectral vegetation indices

The MODIS spectral vegetation indices (SVIs) are spatially and temporally resampled images to be used for consistent comparisons of vegetation activity. SVIs can be used as such because they are dimensionless radiometric measures of vegetation, exploiting the unique spectral signatures of the behavior of canopy elements, particularly in the red and near infra-red (NIR) portions of the spectrum (Huete *et al.* 2002). According to the theoretical basis of the corresponding algorithm (Huete *et al.* 1999), the bidirectional reflectance distribution function (BRDF: MOD43) of each pixel is used to normalize the reflectances to a nadir view and standard solar angular geometry. After normalization the vegetation index compositing routine combines multiple images into a single, gridded, and cloud-free SVI map, taking into account the variable atmosphere conditions, residual clouds, and a wide range of sensor view and sun angle conditions.

Two different vegetation indices are provided in MOD13 datasets: the Normalized Difference Vegetation Index (NDVI, Equation 1) and the Enhanced Vegetation Index (EVI, Equation 2).

Equation 1. $NDVI = \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + \rho_{red}}$

Equation 2. $EVI = G \frac{\rho_{NIR} - \rho_{red}}{(\rho_{NIR} + C1) * (\rho_{red} - C2) * (\rho_{blue} + L)}$

In Equation 2. G is an empirical gain factor and ρ_{NIR}, ρ_{red} and ρ_{blue} are the surface bi-directional reflectance factors of the respective MODIS bands, corrected for Rayleigh and ozone absorption. L is a canopy background adjustment factor addressing different NIR and red radiant transfer through a canopy, and C1 and C2 are the coefficients of the aerosol resistance term which uses the blue band to correct for aerosol influences in the red band. For MODIS products, parameters have been empirically set to L = 1, C1 = 6, C2 = 7.5 and G = 2.5 (see reasons in Huete *et al.* 2002)

Although both indices are considered solid estimators of vegetation activity, they perform differently under similar circumstances, meaning that they capture different vegetation properties. On the one hand, the NDVI permits meaningful comparisons of seasonal and inter-annual changes in vegetation growth and activity since it reduces many forms of multiplicative noise (illumination differences, cloud shadows, atmospheric attenuation, topographic variations, and so on) presented in multiple bands. Yet it has disadvantages in that there is an inherent non-linearity of ratio-based indices with respect to vegetation activity, additive noise of atmospheric path radiances, scale-dependency and asymptotic (saturated) signals over high biomass conditions (Huete *et al.* 2002). While the NDVI has been shown to be chlorophyll sensitive, the EVI is more responsive to canopy structural variations (Gao *et al.* 2000). The EVI was developed to optimize the vegetation signal in high biomass regions, to de-couple canopy background signals and to reduce atmospheric influences (Huete *et al.* 2002). Those are the reasons behind EVI's overall better performance in heavy aerosol, biomass-burning conditions (Miura *et al.* 1998).

According to Huete *et al.* (1999, 2002), the MOD13 algorithm operates on a per-pixel basis and requires multiple observations (days) to generate a composite image. Due to sensor orbit overlap, multiple observations may exist for one day and a maximum of four observations may be collected. This can result in a maximum of 64 observations over a 16-day cycle; however, due to the presence of clouds and the actual sensor spatial coverage, this number will range between 64 and 0 with decreasing observations from higher to equatorial latitudes. The algorithm separates all observations by their orbits providing a means to further filter the input data. Once all 16 days are collected, the algorithm applies a filter to the data based on quality, cloud, and viewing geometry. Cloud-contaminated pixels and extreme off-nadir sensor views are considered lower quality. A cloud-free, nadir view pixel with no residual atmospheric contamination represents the best quality pixel. Only the higher quality, cloud-free, filtered data are retained for compositing. Thus, the number of acceptable pixels over a 16-day compositing period is typically less than 10, especially when one considers a mean global cloud cover of 50 to 60%. The goal is to extract a single value per pixel from all the retained filtered data, which is representative of each pixel over the particular 16-day period. The compositing algorithm chooses among three separate techniques, depending on the number and quality of acceptable observations:

MVC: maximum value composite,

CV-MVC: constraint-view angle - maximum value composite,

BRDF-C: bidirectional reflectance distribution function composite.

The maximum value composite (MVC) is similar to that used in the AVHRR-NDVI product, in which the orbit observation per day and the pixel observation per period of 16 days, with the highest NDVI value, is selected. If at least five, good quality observations are available for a given pixel, then the BRDF-C module is employed to derive nadir interpolated reflectance values from which the SVIs are computed. If there are less than five acceptable values, then the constrained view angle maximum value composite (CV-MVC) module is employed; this module compares the *n* number of observations (*n* being set to 3 to 5 at the moment) with the highest NDVI and selects the observation with the smallest view angle, i.e. closest to nadir view, to represent the 16-day composite cycle. Finally, the MVC technique serves as the backup, such that the pixel with the highest SVI value is assumed to be most representative over the 16-day period marked by less than optimal data quality. All compositing methodologies cause spatial discontinuities, owing to the fact that disparate days can always be chosen for adjacent pixels over the 16-day period. Thus, differences between adjacent pixels may also originate from different days, with different sun-pixel-sensor viewing geometries and different atmospheric and residual cloud/smoke contamination. The BRDF method has the potential to achieve higher spatial consistency through a standard nadir-view interpolation. Unfortunately, vegetation is most active during the rainy (and cloudy) season, even in the deserts, greatly impeding to run the BRDF technique under those circumstances.

MOD15 leaf area index and fraction of absorbed photosynthetically active radiation

Leaf area index (LAI) and FPAR are key state variables in all models of ecosystem productivity, hydrology and biochemistry (Sellers *et al.* 1997); therefore, they are suitable variables for describing ecosystem functioning and for classifying areas into functionally homogeneous units. MODIS LAI / FPAR datasets are level 4, modeled products, derived from MODIS reflectances and ancillary data on surface characteristics, such as land cover type, background and vegetation optical properties. They are produced globally, for periods of 8 days, and are spatially standardized to 1km. Retrievals are achieved by comparing observed radiances (as measured by the sensor) with modeled radiances for a suite of canopy structure and soil patterns that covers a range of expected natural conditions. The set of canopy/soil patterns for which the magnitude of the residuals in the comparison does not exceed uncertainties in observed radiances, is then used to evaluate the distribution of LAI and FPAR values and to specify the most probable value of both variables (Knyazikhin *et al.* 1999).

The algorithm ingests up to 7 MODIS bands to split the tree-dimensional radiative transfer problem into two independent sub-problems (canopy and ground), each of which is expressed in terms of three basic components of energy conservation law: transmittance (for canopy), reflectance and absorbance (for ground and canopy), with the overall goal of producing LAI and FPAR set of values with the same statistical properties as if they were derived from ground-based measurements (Knyazikhin *et al.* 1998). Conceptual setting assumes that solar radiation, scattered from a vegetation canopy and measured by satellite sensors, is caused by interaction of photons traversing through the foliage medium, bounded at the bottom by a radiatively participating surface. Therefore, to estimate the canopy radiation regime, three important features are carefully formulated. These are: (1) the architecture of individual plant and the entire canopy (i.e. leaf density and stem density distribution functions); (2) optical properties of vegetation elements (leaves and stems, which depends on physiological conditions: water status, pigment concentration, etc) and soil; and (3) atmospheric conditions which determine the incident radiation field. The algorithm used allow multiple solutions for the data inversion problem, which refers to the fact that while precise values of upwelling radiances can be inferred from a unique combination of LAI and FPAR values, several combined values of LAI and FPAR can be inferred from the same set of upwelling radiances. As a result, the range of variation of the input variables is limited by using a vegetation cover classification and an additional routine to identify non-physical solutions has been implemented. The ancillary land-cover classification divides global vegetation into six biomes: grasslands and cereal crops, shrub formation, broadleaf crops, savannas, broadleaf forests and needle-leaf forests. Further information on the algorithm can be found in Knyazikhin *et al.* (1998, 1999) and Shabanov *et al.* (2003).

Uncertainties involved in the data inversion process were analyzed by Wang *et al.* (2001). According to these authors, two factors are of major influence on the quality of surface biophysical variables retrieved from remote sensing: uncertainty in the land surface reflectance product and model uncertainty, as determined by the range of natural variation in biophysical parameters not accounted by the model. In the first case, atmospheric and other environmental corrections are critical, while for the second factor, uncertainties heavily depends on the amount, quality and spatio-temporal resolution of available data, as well as on the assumed ecological characteristics of the surface. In the case of MOD15, the later is represented by the possibility of having misclassified an area land-cover type. Although retrieval accuracy cannot be better than the accuracy in the input data (reflectances and the model), quality of retrievals can be influenced by the appropriate use of uncertainty information in the retrieval technique. That has been a central tenet when formulating the data inversion problem. Being so, when model and land-surface reflectance uncertainties are overestimated, the algorithm produces a large number of acceptable solutions; that is, the algorithm fails to converge onto a most probable value for LAI and FPAR. On the other hand, when uncertainties are underestimated the algorithm fails to provide reasonable solutions and/or retrieval quality (the rate of success to prescribe correctly biophysical parameters) decreases. In summary, by an accurate estimation of the overall uncertainty (see also Tian *et al.* 2002a, Shabanov *et al.* 2003), the MOD15 algorithm finds the most 'reasonable' canopy structure (for which LAI is a defining parameter and FPAR a consequent variable) corresponding to the given set of recorded reflectances.

ASSESSING ENVIRONMENTAL CHANGE WITH MODIS-DERIVED EFTS

Environmental change takes form under several, interconnected ways. Its most emphasized dimension is climatic, involving trends of variation in temperature and precipitation, annual averages, maximum and minimum magnitudes and/or seasonal distributions. Another dimension of major concern relates to human activities, as these influence the geographic distribution and composition of ecosystems, as well as the spatio-temporal patterns of resource availability linked to ecosystem processes. The undeniable impact of environmental change on human welfare has converted the subject into a cardinal scientific and political issue, aware as we are of the generally rapid, though regionally variable pace at which it occurs. However, the causes and consequences are quite diverse and involve phenomena operating at various spatial and temporal scales. As Shugart (1998) noticed about pollutants like atmospheric CO_2, a detailed understanding of how these affect individual leaves or plants, under different levels of light, humidity or temperature regimes, does not answer how such responses are translated into alterations of the species (and plant functional types) composition or productivity of the vegetation over a region and over decades. Therefore, scaling in time and space is central to deal comprehensively with environmental change.

Golley (2000) examined the problem grounded in concepts such as system, hierarchy and control. A system is defined as an entity with diffuse, open and definition-dependent boundaries, processing inputs into outputs. Hierarchy means a nested arrangement in which influences propagate up and down across different levels, as well as among systems of similar level (transfers), and control implies some causation process behind an observed pattern. These notions not only make possible a complex realization of spatial heterogeneity but also allow embracing, in a single theoretical model, dissimilar sources of change as we move across the levels of the hierarchy. It may be said that, while upper hierarchical levels provide boundaries and controls to the processes occurring at lower hierarchical levels, these later collect the functional units whose interplay explains the upper level functioning and dynamics, at a cost of adding increasing levels of uncertainty in the process (see Holling 1992, Wu 1999). It is worthy of notice that, as uncertainty propagates upwards, determinism dominates information passage downwards the hierarchical ladder. If one seeks for causality, going from the (most inclusive) upper levels to the (most specific) lower levels seems the right way to do things. Moreover, cross-scaling implies bridging concepts of different disciplines, yet preserving the particular contribution of each one to the subject. Sometimes such a linkage gains explanatory power or operationality by coining a new concept.

Golley (2000) rightly pointed that landscapes and ecosystems are not components, of higher and lower order respectively, of a single hierarchical spatial arrangement., However, when he defined a landscape as being an ecosystem, he might have failed to identify their different places in ecological science. A given area may be described in either term, depending on which phenomena have been chosen for consideration. Nevertheless, if necessary, one may depict a landscape pattern as a collection of ecosystems or vice versa. The difference between the ecosystem and the landscape approach resides, in my opinion, in the output for which inputs and processes are to be ascribed: if the output is concerned with spatial differentiation, that is the reciprocal action of biota and its non-living environment to produce a distinguishable spatial pattern (i.e. composition plus arrangement of spatial objects), the most suitable conceptual framework is provided by the landscape. The ecosystem, on the contrary, provides the best context to emphasize what emerges functionally and/or structurally homogeneous by synergy between the biotic and non-biotic components of an ecological assembly. For additional insights about I refer to Naveh (2005), Moss (2005) and Shugart (1998). This differences notwithstanding, a closer look readily reveals the strong complementary of the landscape and ecosystem concepts. Ecosystem attributes can only be fully accounted for when one considers the influence of spatial heterogeneity on the nature and rate of its processes. Meanwhile, processes within ecosystems and transferences among neighboring ecosystems interact to produce and enhance spatial patterning (see Turner & Chapin 2005). Though it has an evident ecosystemic bias, the concept of Ecosystem Functional Types seems to be promising for linking landscapes and ecosystems.

Paruelo *et al.* (2001) coined the notion of EFTs with the ultimate goal of assessing the impact of environmental change on vegetation, taking advantage of the highly dynamic relation between functioning and environmental controls. As I mentioned, time-series of AVHRR-derived NDVI were used to approach seasonal patterns of carbon assimilation. Since methodological and ecological factors produced a classification in which each functional type represented a mosaic of physiognomically-defined units, EFTs are both ecosystems and landscapes, but defined on the basis of a common functional criterion. If we subscribe to the idea that the chosen functional criterion and the environment are robustly connected, by recognizing the drivers behind the spatial distribution of each EFT, we should be also identifying those drivers of major relevance producing the associated landscape pattern (i.e. a set of physiognomic units, each following a given probability density function). At the same time, the functional pattern itself, that is, the seasonal variation of some ecosystem-process descriptors, is expected to be related to a set of perhaps different environmental variables, revealing the processes of higher hierarchical order which control processes at the level of the EFTs. Additional examination of the relationship among spatial and seasonal environmental drivers would offer insights on the ecological linkage among determinants acting within the landscape and ecosystem integrative frameworks.

The classification procedure enunciated by Paruelo *et al.* (2001), and later replicated by Alcaraz *et al.* (2006), does not fit quite well the scientific role that I propose for EFTs. The authors reduced the total observational vector per pixel (360 counts of NDVI, one each 10 days and covering the period from 1982 to 1991) to a set of three average traits (the annual integral, the relative annual range and the date of maximum NDVI) describing the index seasonal behavior. Based on those traits, pixels were assigned a type by maximum likelihood. Implicit in this procedure was the assumption of stable EFTs throughout the period under analysis, inter-annual variation being the product of normal oscillations around a mean seasonal curve. It could be alleged to favor the procedure that, (a) given the relatively short span of the time-series, there was no reason to believe that a pixel assigned to a type A had changed from B to A (or vice versa) in 10 years, and (b) the pixel size (64 km^2) support arguments in the same direction because the bigger the pixel, the greater the changes needed to alter its functional pattern. *Nevertheless, provided that functioning is a very responsive attribute of the ecosystems under the influence of highly dynamic environmental drivers, such as climate and land use, one should expect the spatial distribution of functional types to be as dynamic as the drivers acting upon it.* This tenet asks for a classification procedure performed on a yearly basis, in which the stability throughout the time of the type to be assigned to a pixel is not assumed *a-priori*, but the result of a multiyear comparison among independent and similar classifications. Classifying EFTs on a yearly basis also eliminates suppositions (a) and (b), allowing the use of datasets of short temporal coverage and variable pixel size (such as those of MODIS-Land) as information sources.

Deriving EFTs from MOD13 and MOD15 time series add analytical strength to the concept: functionally homogeneous areas can be obtained for several spatial resolutions, either using individual indices and/or parameters, or combining them to benefit from their complementarity. In each case, different aspects of ecosystem functioning are expected to emerge, as well as distinctive patterns of interaction with meaningful habitat factors. The effect of spatial resolution is neither trivial nor evident; by organizing EFTs obtained at different resolutions, in a nested hierarchical arrangement, environmental drivers operating at each level can be identified and related to the corresponding processes of spatial differentiation or to the structural features typifying at that level the dominant vegetation. However, the mere change of pixel size does not guarantee significantly different spatial resolutions. Pixel coverage should increase or decrease to reach a critical size so that new patterns become evident, since the grain size of spatial heterogeneity does not vary monotonically along the scaling ladder (Wu 2004). Likewise, spatial resolution also implies the range of variability taken into account. By windowing the entire study area into sub-areas of different coverage and ecological characteristics, the researcher may expect to redefine maximum and minimum values for the traits describing functioning, as well as to unfold specific patterns of variation not clearly manifest at the scale of the total area.

FINAL REMARKS

So far I have presented a new line of theoretical and methodological development based on the concept of Ecosystem Functional Types. In this, the tenets of pixel contents being dynamic and the notion of the existence of functionally-homogeneous areas are crucial. The novelty of my approach is also rooted in the methodological innovations to handle efficiently the effects of ecological uncertainties and remote sensing errors when dealing with the interaction between ecosystem function and structure, and the effect of habitat factors on the function/structure interplay. My conceptualization of the problems, if inserted in a theoretical framework of hierarchical patch dynamics, offers favorable conditions for spatial and temporal scaling and for linking the processes occurring at the ecosystem and landscape contexts.

For the purposes above, I propose the use of suitable MODIS-Land datasets, MOD13 and MOD15, on a yearly basis. Regardless of MODIS's improved sensor and data processing, a preliminary stage of validation for the functional classes so-obtained is needed since several sources of uncertainty are present in their products. Moreover, the model inversion yielding MOD15 functional parameters (LAI and FPAR) rely on a land-cover classification whose accuracy varies from one region to another. I believe that, to a great extent, the emphasis on seasonal patterns, instead of on absolute values, will ameliorate this problem. Nevertheless validation is a must as a way for assessing the consistency of (a) the landscape patterns EFTs represent and/or (b) the set of habitat factors driving functional patterns. This is validation based on classification results. If consistency can be achieved, ecosystem functional types, based on MODIS-Land information, will make a powerful tool for scaling the response of the vegetation to environmental change.

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Table 1. Products of the MODIS-Land discipline, after Parkinson and Greenstone (2000). L2G: Geolocated, calibrated, atmospherically corrected and gridded (spatial composite); L3: Gridded, temporal composite; L4: Modeled product. NPS: Net Photosynthesis, NPP: Net Primary Productivity

Dataset	Processing level	Product ID	Resolution	
			Spatial (km or °deg)	Temporal (d)
Surface Reflectance	L2G	MOD09	0.25, 0.5	1
	L3	MOD09	0.25, 0.5	8
Snow Cover / Sea Ice	L3	MOD10	0.5, 1, 0.05°	1, 8, 30
Land surface temperature	L3	MOD11	1, 5	1, 8
Land Cover / Dynamics	L3	MOD12	1, 0.05°	365
Vegetation Indices (SVIs)	L3	MOD13	0.25, 0.5, 1	16, 30
Thermal anomalies / Fire	L3	MOD14	1	1, 8
LAI / FPAR	L4	MOD15	1	8
NPS	L4	MOD17	1	8
NPP	L4	MOD17	1	365
BRDF / Albedo	L3	MOD43	1, 0.05°	16
Vegetation cover conversion	L3	MOD44	0.25	96
	L4	MOD44	0.5	365

Figure 1. The MODIS project includes land, ocean, atmosphere and calibration disciplines. In the figure, data processing for the MODIS-Land discipline products. After Parkinson and Greenstone (2000).

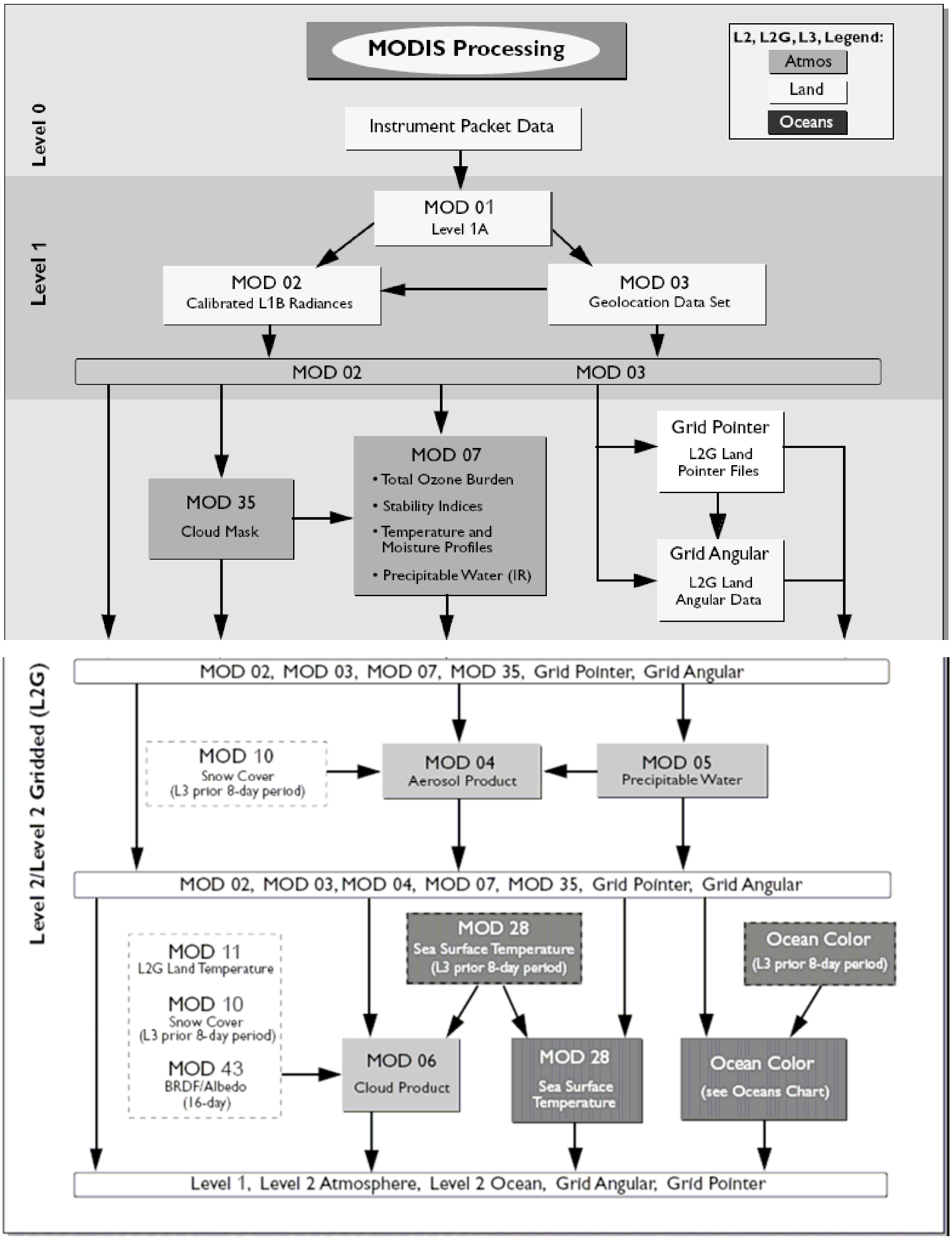
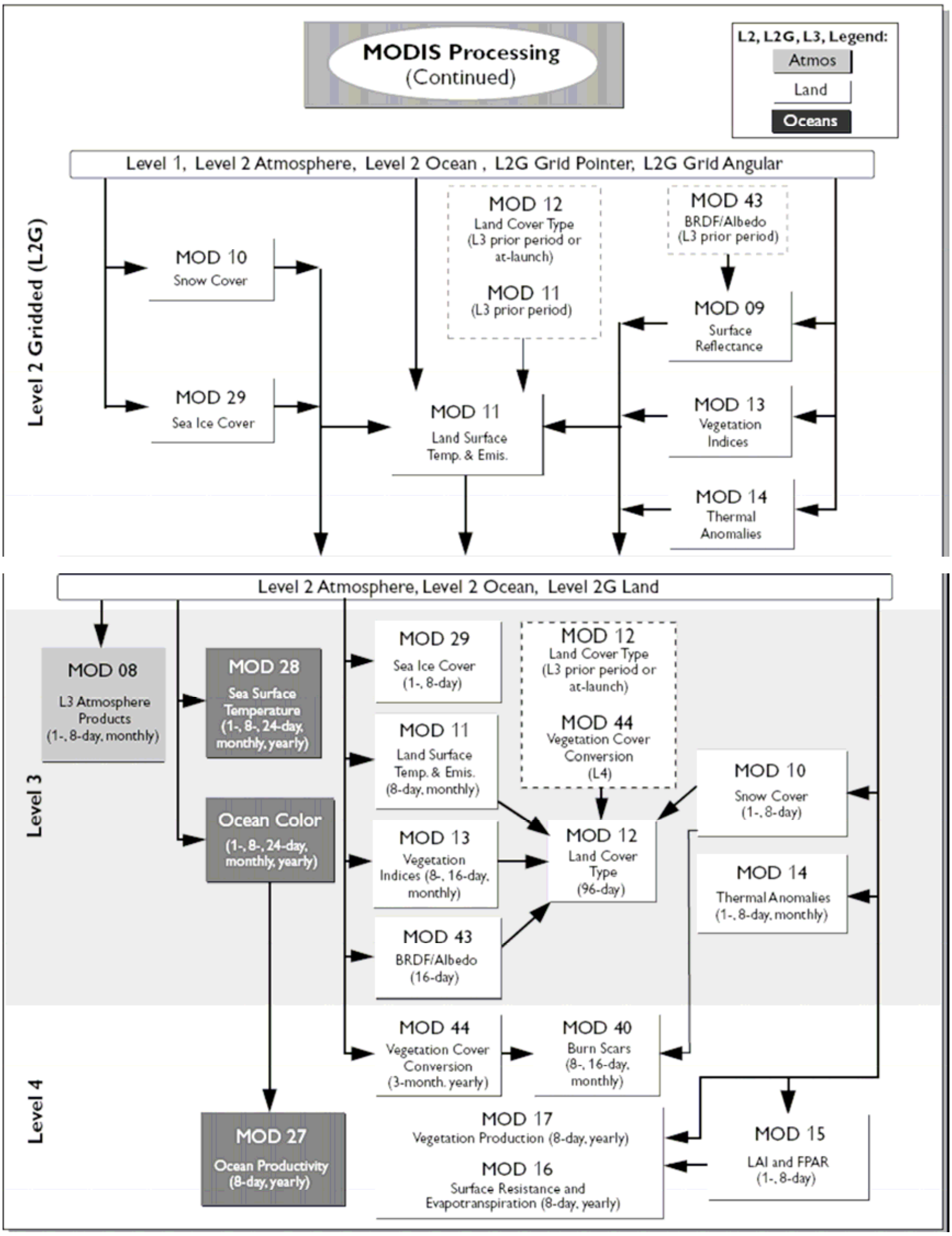


Figure 1. Continuation.



CHAPTER 2. LANDSCAPE PATTERNS AND DYNAMICS IN THE BASALTIC TABLELANDS OF SOUTHERN BRAZIL

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ABSTRACT

In the extensive tablelands, ca. 100,000 km^2, modeled on Mesozoic lava flows in the southernmost Brazilian state of Rio Grande do Sul, the generalized occurrence of grasslands interspersed with different types of forests confer onto the area a distinctive mosaic vegetation pattern. In this report we focus on the identification and characterization of landscape units in a selected area of the basaltic plateau, taking into account general aspects of topography and soil forming processes. Then we scale-down to selected windows of about 56 km^2, in which a finer resolution analysis will reveal the interplay of regional drivers with local habitat factors on the production of the mosaic pattern of grasslands and forests.

Main questions concerning the subject matter include: 1- Which are the dominant patterns of vegetation distribution over the basaltic tablelands? 2- Are these patterns related to coarse-grain determinants of spatial heterogeneity, such as tectonics, climate, land-forming and soil-forming processes? And if so: 3- How the landscape-defining

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patterns relate to local scale drivers of ecosystem turn-over, such as cattle grazing and fire in relation to forest tree seedlings? 4- What would be the causal linkages among coarse- and local-scale patterns?

Landscape type identification and characterization was carried out in four steps: 1- A preliminary assessment, based on ground observations, ancillary data analysis and the visual inspection of remote imagery, included criteria of different kinds (landforms, soils, vegetation and land-use patterns) to determine the extension and general characteristics of the tablelands, as well as major landscape motifs within the area. In order to corroborate the results of our assessment, we stratified image classification as follows: 2- We identified major topographic domains on the basis of topographic traits derived from the Digital Terrain Model (DTM). 3- Within the domains deemed as belonging to the tablelands, a classification based on vegetation / land-use pattern recognition was performed. 4- In the final step, we identified areas with similar topographic domain and vegetation / land-use pattern, and compared them with the landscape types recognized during the preliminary assessment. In each 'homogeneous landscape' we selected windows of about 56 Km^2 for high resolution pattern-analysis based on LANDSAT images and terrain features.

From the spatial association of terrain features, soils, land-use and vegetation, we identified three basic landscape types and broadly defined their spatial domain: 1- the *Planalto das Missões*, 2- the *Vacaria* tablelands and 3- the *Cambará – Tainhas* tablelands. Within the three landscape types high-resolution pattern analysis provided strong evidence that the distribution of land-use forms and natural vegetation units is connected with soil-forming and geomorphic processes. In general terms, the remaining natural grasslands prevail in areas where terrain and soil features suggest relics of an old pediplanation surface. These grasslands share their environmental space with cash-crop agriculture and pastures for cattle grazing. Natural forests, in turn, dominate wherever

geomorphic agents have rejuvenated the landscape and seem to share their environmental space with commercial forestry.

However, for understanding the development of the forest-grassland pattern, fire disturbance cannot be ignored. Therefore, fire frequency and intensity have to be considered as an attribute of the grasslands varying in close connection with the functional heterogeneity of the ecosystems. The impact of the fire regime on the ability of forests to expand, need to be considered as well, in relation to the functional heterogeneity of the natural forests in the area.

Key words: Pattern-analysis, regional landscape types, terrain features, subtropical grasslands, semideciduous forests, montane forests.

Running title: Landscape patterns in Southern Brazil

INTRODUCTION

Natural mosaics of forests and herbaceous ecosystems occur in several areas of the world. A few examples are the extensive tropical savannas intermingling with semideciduous and evergreen forests (see Furley *et al.*, 1992), the high-altitude Andean grasslands (*páramos*) mixed with *Polylepis* dominated forests and montane forests (Monasterio, 1980), or the coexistence of subtropical grasslands (*campos*) with evergreen Montane forests and semideciduous forests in the tablelands of Southern Brazil (Pillar, 2003 and references therein). The identity of the factors determining the occurrence of either type of vegetation is still a matter of debate. Although the limit between grasslands and forests at high altitudes seems to relate to mean ground temperatures (Koerner & Paulsen, 2004), in the case of the analogous ecosystems at the tropical lowlands the more apparent factors are water availability and nutrient status (Sarmiento & Pinillos, 2001). In the tablelands of Southern Brazil, frequency and intensity of disturbance (fire and cattle grazing) have been pointed out as regulating both the current distribution and the spatial dynamics of regional ecosystems (Pillar, 2003).

The presence of forest-grassland mosaics is a puzzling matter for a landscape ecologist since the patchy motif implies a highly dynamic ecosystem turn-over in the space. Correlatively, a high spatial turn-over may respond to far-from-equilibrium conditions in the landscapes, for which most active processes of spatial-pattern change are expected. Under those circumstances, the concepts of location and spatial pattern acquire major relevance, not only to uncover the underlying explanatory mechanisms, but also to determine their ecological range of validity. All of these are critical issues for the Landscape Ecology and set the most appropriate scenario to debate the role and specific scope of the discipline.

In this report we deal with the identification and characterization of landscape units in a selected area of the basaltic plateau of Southern Brazil, in the north portion of the state of Rio Grande do Sul State, where subtropical *campos* and forests coexist. At the regional scale, general aspects of topography and soil forming processes will be linked to underlying geomorphic mechanisms and explained by long-term geologic events and climatic changes. After this, we will scale-down to selected windows of about 56 km^2, in which a finer resolution will reveal the interplay of regional drivers with local habitat factors. The influence of the interplay on the distribution of the main vegetation cover will be discussed in terms of composition and configuration. By doing this analysis, we aim at the following goals: 1- to add to the comprehension of the regional patterns of forest – grassland distribution over the basaltic plateau in Southern Brazil, 2- to frame this problem in the more general context of the global forest-grassland mosaics, and 3- to stimulate further debate on the nature and definition of the landscape in the domain of the ecological sciences.

The theoretical corollaries of landscapes and ecosystems

There is still going on a very active debate on what is science's basis for defining Landscape Ecology (Weins & Moss 2005). The landscape is a central issue for disciplines of different kind, such as geography, architecture, ecology and the arts, although the set of relationships the term implies varies from one discipline to next with their different purposes, methods and conceptual backgrounds. In all cases, however, the notion of landscape refers to areas ranging from a few hectares to several square kilometers, or even larger, recognizable in its singleness by a *patterned* arrangement of heterogeneous units in space (King 2005). The adjective 'spatially-patterned' is defined after Pastor (2005) as the quality of having non-random composition and configuration in space.

Zonneveld (2005) identifies two different approaches to this matter from the ecological field. The first corresponds to the European school of landscape science and is deeply rooted in the idea of the 'integral land survey', which in turn aims to combine notions coming from soil science, geomorphology and vegetation science. The second approach, identified as the North American school, developed from the early 1980s as a spatially explicit branch of ecosystem ecology (see, for instance, Golley 2000, Turner 2005, Turner & Chapin 2005, Weins 2005). For this view the landscape is "an heterogeneous area composed of a cluster of interacting ecosystems, that is repeated in similar form also elsewhere (Forman & Godron 1986). Although both approaches are rather complementary, they have largely evolved as two independent 'solitudes', notwithstanding the usage of a common set of tools such as GIS, spatial statistics, spatially explicit modeling, remote sensing and so forth (Zonneveld 2005, Naveh 2005).

According to Weins (2005), to unify landscape ecology is to recognize the essential *sameness of the phenomena* to be studied by the discipline. Yet a scientific phenomenon is always an intellectual construct, the product of raising questions and choosing, among those we are able to reach, the subset of topics more rewarding to consider. If the landscape' central notion is that of a 'patterned arrangement of heterogeneous units in the space', then the field should focus on comprehending the system of causalities and processes, named governing principles, responsible of that pattern. That is to say, the main goal of Landscape Ecology is the placing of the governing mechanisms into the ecological realm of spatial patterns.

Paraphrasing White and Brown (2005), to understand how ecological processes play out on an underlying template of abiotic and biotic environmental variation, it is first necessary to understand the causes behind the variation, that is, to reveal how is the template structured or organized that way and how does it change over time. The statement confronts us with a variety of factors of very different nature and scale, which interact to produce a particular spatial motif. These factors are indeed scale dependent (long, medium and short-term) expressions of tectonics, hydrology, climate, soil development, vegetation dynamics and human influence (see Sarmiento & Pinillos 2001, Swanson et al. 1988). Their interaction produces a mosaic that is unique, yet still amenable to typification.

Long- and medium-term processes may exceed the spatial and temporal scale at which ecosystem phenomena regularly express, while medium to short-term processes, like erosion and deposition dynamics, land-use changes, horizontal water balance and succession, fall well within the temporal window of ecosystem science for incorporation into the spatially explicit framework of ecosystem research (see Shugart 1998, Turner & Chapin 2005). As such, what make the European and American schools of landscape ecology so different may well be to a considerable extent a matter of the temporal resolution of the data used to interpret a particular spatial pattern and process. Needless to say is that both approaches are quite interdependent. However, while one may define an ecosystem irrespective of its spatial context, i.e. as an abstraction without a precise spatial domain (Shugart 1998), the same is not valid for the landscape. The spatial relationship among its constituent parts is what supports the landscape's very existence. The landscape is an abstraction with an explicit spatial domain, because its extent and location clearly comes from its definition (see King 2005).

We subscribe to the tenet ecosystems and landscapes are theoretical expressions of different, yet complementary natural phenomena. Both notions can be approached from a systemic perspective: open entities in which energy, matter and information inputs are processed into outputs (Golley 2000). To ecological science, ecosystems as much as landscapes emerge from the reciprocal interaction between organisms and habitat factors, physical-environmental and land-use related. However, while outputs for ecosystem processes refer to temporal, point-based patterns of matter and energy exchange and/or of biomass and resource allocation, landscape processes produce the differentiation in the space of a given set of ecological parameters and/or variables. The convergence of both approaches results from the unsubtle effect landscape structure has on the distribution and abundance of organisms, communities, abiotic factors and, hence, ecosystems (Reynolds & Wu 1999, Sarmiento & Pinillos 2001, Swanson & collaborators 1988, Turner 1989, Turner & Chapin 2005), as much as from the counteracting influence of ecosystem processes on the generation, maintenance and enhancement of ecological heterogeneity in the space (White and Brown 2005, Thomas 2005).

There is a tradition in the ecological science that considers the landscape a level in the hierarchical system of the ecological systems, a system in which ecosystems and biomes would neighbor the landscape as levels of lower and upper order respectively. King (2005) argues against this assumed organizational ladder, which he ascribes to an extrapolation to the ecological science of the traditional biological hierarchy. Like King (2005), we believe the hierarchical arrangement better describing a landscape emerges not from a rock-solid convention, but from the ecological problem to be tackled. The levelness of the landscape, if not derived from a hierarchy of ecological entities, should come from the nature and the inherent spatio-temporal scale of the phenomena under analysis. For instance, if one wants to explain different rates of matter and energy flow across an area, it is perhaps appropriate to consider the landscape as a complex of ecosystems as its functional units, then giving these ecosystems an appropriate spatial domain. However, a landscape may also be depicted as a nested hierarchical system of soil units, land-use covers, landforms, plant covers, plant functional traits, populations or even landscapes of lower order. Thanks to its multi-faceted nature, the proper recognition of landscape' patterns serves a wide spectrum of ecological disciplines, Ecosystem Ecology included (see, for instance, Burke et al., 1990; Burke, 2000; Walker, 1994), but in no case such a multi-faceted nature would prescribe the disaggregation of the landscape ecology into the spatially explicit branches of the other disciplines.

Subtropical campos and forests in Southern Brazil: A puzzling matter for a landscape ecologist

The extensive tablelands of ca. 100,000 km^2, modeled on Mesozoic lava flows in the northern half of Rio Grande do Sul can be considered a large and in many ways homogeneous eco-region. The generalized occurrence of grasslands (*Campos*) interspersed with different types of forests, under a subtropical to mild-temperate humid climate, confer to the area a distinctive mosaic pattern. This pattern is evident when observing it at the 1km^2 spatial resolution MODIS imagery and it is also apparent in LANDSAT 7TM imagery. During the last several decades forestry and agriculture have played an increasingly dominant role shaping landscape mosaics. However, local land uses apparently occupy the area closely following the constrains imposed by the environmental setting. As a result, original distributional patterns of natural vegetation are still evident everywhere. This notwithstanding, the ecological determinants behind the coexistence of campos and forests, in this somehow climatically and geologically homogeneous eco-region, have not been fully disentangled (see, for instance, Lindeman & Ferri 1974, FIBGE 1986, Pillar 2003, Oliveira & Pillar 2004).

The widely accepted interpretation considers upland *campos* to be remnants of a colder and drier steppe climate that would have come about during the Late Pleistocene and Early Holocene (Schultz 1957, Klein 1975, Bigarella & Andrade-Lima 1982, Waechter *et al.* 1984, Pillar & Quadros 1997, Pillar 2003, Behling & collaborators 2002, 2004, 2005, 2007). Under the current wet subtropical regime forests are considered the climatic vegetation, forests and grasslands distribution is thought to be transient, and the mosaicked pattern, an intermediate stage on the regional landscape evolution forced by the climatic equilibrium. According to this scenario, current landscape patterns are the result of the ongoing, but as yet incomplete, process of one major physiognomic type (forests) advancing over the other (*campos*). Such a process would have been controlled by grassland fires, since the time early in the process of forest expansion (Behling et al. 2004, 2005, 2007), and by the introduction of cattle in the 17th and 18th centuries (Goulart, 1978). According to Pillar (2003), the conversion of natural grasslands into rangelands slowed and even deactivated forest expansion by enhancing the mortality of young trees and seedlings. Factors directly responsible (prescribed fires, cattle consumption and cattle trampling) rendered furthermore sharp transitions between the forest groves and their neighboring grassland matrices. During the last decades, the conversion of extensive areas over the tablelands into managed pastures, agriculture and forestry have also made of land-use change a forceful control on the regional dynamics of spatial patterning (FIBGE, 1986, 1990; Bristol, 2001).

Main questions concerning the subject are: 1- Which are the dominant patterns of vegetation distribution over the basaltic tablelands? 2- Are these patterns related to coarse-grain determinants of spatial heterogeneity, such as tectonics, climate, land-forming and soil-forming processes? And if so how? 3- How landscape-defining patterns relate to local scale drivers of ecosystem turn-over, such as cattle and fire controls on forest seedlings? 4- What would be the causal linkages among coarse- and local-scale factors? These questions, addressed from the integrative perspective of down-scaling the regional processes into local-specific landscape motifs, should provide fresh insights into the complex nature of the subtropical mosaics in the basaltic plateau.

METHODS

The region bounded by 27° to 29 ° 30'S and 55 ° to 49 ° 30'W covers the northern half of Rio Grande do Sul (Map 1). For the area, ortho-rectified, atmospherically corrected and shaded Landsat images (Bands 5, 4 and 3, from May to October 2001, compatible scale 1:250,000, geographical system SAD69) and the corresponding digital terrain model (DTM, compatible scale 1:100,000, geographical system WGS84), were downloaded from the official site of the Brazilian Agency for Agricultural Research (Empresa Brasileira para a Pequisa Agropecuária, EMBRAPA) http://www.relevobr.cnpm.embrapa.br. The DTM of EMBRAPA is a ground-controlled terrain model, based on the Shuttle Radar Topography Mission DEM, from which information gaps and spurious values have been removed. Technical information on the process of correcting, geo-referencing and mosaicking 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.

Landscape types identification and characterization was carried out in four steps: 1- A preliminary assessment, based on ground observations, ancillary data analysis and the visual inspection of the imagery, included several criteria (landforms, soils, vegetation and land-use patterns) to determine the extension and general characteristics of the tablelands, as well as major landscape motifs within the area. In order to corroborate the results of our assessment, we stratified image classification as follows: 2- We identified major topographic domains on the basis of topographic traits derived from the DTM. 3- Within the domains deemed as belonging to the tablelands, a classification based on vegetation / land-use pattern recognition was performed. 4- In a final step, we identified areas with similar topographic domain and vegetation / land-use pattern, and compared them with the landscape types recognized during the preliminary assessment. Conclusions on the accuracy of the assessment were drawn from the comparison.

Landscape types preliminary assessment

Several field trips were taken to the region, starting from the second half of 2003 to the first half of 2005. Key profile features of the dominant soil, prevalent land-use, mosaic grain-size and plant-cover type composition were recorded. Since this survey was aimed to identify the composition and arrangement of local and regional landscapes, rather than to assign an exact type of plant-cover to individual pixels, our field observations were general and broad, located within the images on the basis of well-known landscape markers such as road-crosses, road - river intersections and townships. We complemented this data with more specific ground-proofing points, whose precise location was recorded in terms of coordinates in the geographical WGS84 system. From the analysis of field data, ancillary thematic maps (FIBGE, 1986) and the visual interpretation of false-color composites of the Landsat bands (5, 4 and 3 for the red, green and blue channels, respectively) (Jensen, 1996; Eastman, 2006), we developed a preliminary assessment of regional landscape types. We based the interpretation of false-color composites on pattern, which according to Lillesand & Kiefer (1994) and Jensen (1996) can be apprehended from unit size and shape, shadow, tone, texture, location and association.

Topographic domains in the study area

For step 1 we extracted four topographic features from the DTM: mean altitude, relative altitude, surface ruggedness and slope. Mean altitude and surface ruggedness were estimated for each pixel as the altitudinal average and the standard deviation based on running windows of 41 x 41 units in which the pixel was the center. Relative altitude was obtained by subtracting mean altitude from the DTM altitude of the reference pixel. Slope was calculated (in degrees) as the first derivative of the altitudes in the DTM. We partitioned terrain topography into these descriptors since they are indicators of land-forming processes of different nature and spatial scale. Mean altitude, for instance, is mainly the product of tectonics and defines the position of a pixel in the broad regional hypsithermal and potential energy gradient, while relative altitude is mostly a product of local land-forming processes and describe pixel position in spatially-restricted toposequences that determine drainage and erosion. Likewise, surface ruggedness indicates the rates at which soil stripping and dissection occur in a given area, while slope is clearly related to the intensity of erosion/aggradation processes in the pixel surface. In the particular case of the basaltic plateau, these terrain features have been proven essential by Potter (1977) and Almeida et al. (2000) to delimit and interpret the distribution of main soil and landscape units. We submitted the topographic variables to the iterative and self-organizing ISOCLUST classification routine. ISOCLUST is a modification of the widely known ISODATA routine (Ball & Hall, 1967) in which the preliminary assignment of the pixel to the classes has been optimized in order to reduce the number of iterations needed to obtain stable results. For a detailed overview of the routine and how it differs from the original ISOCLUST see Eastman, (2006). In both, the ISODATA and the ISOCLUST routines, pixels are assigned to *G* groups following criteria of minimum variance within groups and maximum variance between groups. We ran the routine several times, to produce various maps with different *G* numbers of classes. Since we regard soils as good indicators of dominant geomorphic processes in a region, the classification with greater agreement with the regional map of soils (BRASIL 1973) was then selected. From the classes so obtained, we considered as part of the tablelands those with average altitude higher than 300m, altitude standard deviation lower than 40 and average slope lower than 6 degrees, all of which mirror the gently undulating surfaces on top of the basaltic plateau. The chosen classes served thereafter to mask Landsat bands in order to perform the following step only on the geographical domain corresponding to the tablelands.

Landscape patterns in the basaltic tablelands

Given the key elements of pattern formulated by Jensen (1996) and Lillesand & Kiefer (1994), pattern is a property dependent on the context of the pixels whose capture often requires some degree of generalization and detail removal. For this step, we extracted information regarding association and tone by submitting each band to an image generalization procedure, the Gaussian smoothing (Eastman, 2006; Lee, 1983), which outputs a weighted average of a given pixel's neighborhood, with the average weighted more towards the value of the central pixels. In contrast to the mean filter's uniformly weighted average, this generalization method provides gentler smoothing and preserves edges better than a similarly sized mean filter. Also independently for each band, texture was estimated from the standard deviation of each pixel's neighborhood. In both procedures, pixel neighborhoods were windows sized 7 x 7. In the sequel we subjected the six pattern-descriptors (two per Landsat band) to the iterative, self-organizing routine of classification, ISOCLUST (Eastman, 2006). As in the case of the topographic traits, we ran the routine several times, produced as many maps with different *G* numbers of classes and selected the one which predicted best land-use and vegetation types recorded at selected ground-proofing points.

At this point, we had hierarchically subdivided the study area twice, the first time to separate the tablelands from other geographical realms and the second to segregate dominant landscape units within the tablelands. The first spatial partition identified landscapes of first order or regional topographic domains (TDs), while the second partition delimited spatial domains determined by land-use / vegetation. The comparison of these results with our preliminary assessment was then performed rather simply, by tracing several transects in the direction of the main climatic and topographic gradient. Along these transects we checked whether there was a significant correspondence among topographic domains and dominant forms of land-use and vegetation types, and whether such a correspondence agreed with the patterns predicted by our initial assessment. Areas with consistent correspondence among topographic and land-use domains were interpreted as being dominant landscape types (of second order) within the tablelands.

In each landscape type over the tablelands domain we selected a representative window of about 225 km^2, in which image pattern analysis and Landsat bands classification were repeated. While we framed regional landscapes within long-term and extensive geologic, geomorphic and climatic dynamics, we characterized landscape units in each window in terms of the topographic traits, soils, landforms, vegetation and dominant land-use. Although we turn to land-use information to infer the potential and constraints of the environment for the biotic elements of local ecosystems, whenever possible we focused on the linkage between natural vegetation, soil and geomorphic processes. From the singularities and commonalities found when we compared second-order landscapes, we drew conclusions regarding the influence of the regional environmental setting on local landscape patterns and on the associated processes of spatial patterning.

RESULTS

Regional landscapes in the tablelands at first glance

A synthesis of field data, thematic literature and visual pattern-analysis on the Landsat images led to the division of our study area into the sub-regions shown in Map 2. The first partition sets apart the lowlands (unit E) from the spatial domain of the basaltic plateau, while the second partition separates the rather rugged surface of the Sierra domain (unit D) from the smoother areas of the tablelands (units A, B and C). As units D and E fall beyond the scope of this paper, we restrict our presentation to the distinctive features that distinguished units A, B and C in the tablelands domain.

The vastest unit A corresponds to the locally known '*Planalto das Missões* ', extending over an altitudinal range from ca. 200 to 800 m asl, on basic effusive rocks. In the low resolution Landsat composite (Map 2, proximate pixel size: 0.13 km^2), the corresponding area exhibits tones ranging from slight red (bare soil) to full green (for the most actively growing winter crops). Yellowish brown and dark green colors identify the areas under remaining *campos* and semideciduous forests, respectively. Regarding the *campos* in the *Planato das Missões*, it is worth mentioning the outstanding presence of grasses of the *Aristida* genus (mainly *Aristida laevis* (Ness) Kunth and *Aristida jubata* (Arechav.) Herter) forming a sparse, emergent-like layer in the grassland canopy, which gives to the grassland a distinctively uneven, heterogeneous aspect. *Aristida* is absent from the *campos* of other units in the tablelands. From the land-use viewpoint, unit A comprises a highly intensive agricultural system, mainly developed on former natural grassland, in which large farms, mechanization and agrochemicals intensive use are all distinguishing features. Main winter crops, which are grown mostly on the lateritic soils, are forages and cereals (e.g. ryegrass, wheat, oat, barley and alfalfa), while soybean and corn characterize the summer cycle.

Unit B encapsulates the agricultural area surrounding Vacaria city, appearing in the composites mosaic with tones ranging from light red to light brown. From the physical environment viewpoint, brown lateritic soils, of variable depth and covering approximately half of the area, develop on basalts and marginally (to the east) on acid effusives of the rhyodacites type. Younger soils occupy ill-drained bottomlands and rocky outcrops. The altitude ranges from 800 to ca. 1000 m asl. Natural vegetation comprises a matrix of subtropical grasslands (dominated by species of the genera *Andropogon*, *Eragrostis*, *Briza* and *Paspalum*) interspersed by a net of *Araucaria*-dominated forests (Waechter *et al.* 1984). Land-use has extensively led to the replacement of natural grasslands by cash crops (cereals, forages and pomes). Areas of shrubby vegetation (locally known as *vassourais*) are not infrequent, seemingly indicating fallows, overgrazing, recent deforestation and perhaps an ongoing process of forest advance over *campos*.

Unit C corresponds to the easternmost extension of the basaltic plateau, ranging from ca. 1000 to about 1200 m asl. Unlike the previous units, agriculture is a marginal activity in this area, while forest plantations and cattle raising are dominant. Evolving on acid effusive rhyodacites and rhyolites, dystrophic soils of the Entisol order occupy most of the area. Although *Campos* and montane forests, both floristically similar to those of unit B, are still the dominant components of the distinctive natural vegetation mosaics, the general landscape has suffered conspicuous transformation processes: extensive pine plantations are nowadays taking over the natural grasslands, while exotic species (such as the ryegrass) increasingly replace native grasses leading to a gradual substitution of the original subtropical *campos* by semi-natural and/or managed pastures. For a succinct floristic description of the regional grasslands and forests, see Klein (1975) and FIBGE (1986).

The three landscape types on the tablelands share several traits, like the prevalence of large rural properties, the rather extensive occurrence of dystrophic soils and the coexistence of physiognomically contrasting kinds of natural vegetation: forests and grasslands, in an area whose climate has been thought to be typical of forest lands (Klein 1975, Pillar 2003, Schultz 1957). From the land-use viewpoint, large holdings arose from the post-Columbian human occupation dynamics based on extensive cattle raising. However, the overall context of unfertile soils has kept the ownership structure largely unchanged (Bristol 2001). Dystrophic soils, in turn, result from a long time evolution on a tectonically stable surface, most probably under humid regional climates. In spite of their nutrient limitations, some of these soils (Oxisols) sustain cash-crop production since they are deep and prone-to-mechanization, and their lack of fertility can readily be overcome with heavy inputs of fertilizers. Mosaics of grassy wetlands and forests are restricted there to the bottomlands, where they share the area with small-size farming and cattle raising. Montane forests seem to dominate over the rocky outcrops and shallower soils of the higher tablelands while subtropical grasslands tend to occupy the older, more leached soils over the plateau's stable surfaces.

In spite of these major trends, there is no a clear-cut relationship between soils and vegetation types. Fast-growing pine plantations, secondary grasslands and *vassourais* (shrublands) extend over different classes of soil, geomorphic units and natural vegetation types, rendering a fuzzy picture of how land-use dynamics altered the original spatial patterns. Let us take forestry as an example. Since older tracks of commercial forests mostly occur on the shallower, lithic soils of the higher tablelands, one could assume that the activity started by replacing the montane forest wherever it had been logged. However, large tracks of young pines are now developing and extending onto what seems to be natural *campos*. Likewise, secondary grasslands ('secondary' for their higher frequency of woody elements and exotic grasses and lower native grasses richness) might well have resulted from either overgrazing on natural *campos*, the introduction of exotic species, or pasture implantation after deforestation. The *vassourais* have neither an obvious ecological interpretation: they are probably suggesting disturbance, as in the case of agricultural fallows and forest secondary successions. But they may also identify areas where disturbance regimes related to fire and grazing receded, giving an opportunity to forest expansion over the *campos*.

Topographic domains and landscape patterns from image classification

The subdivision of the study area into broad topographic domains (TDs, Map 3) produced a picture of spatial heterogeneity rather similar to that presented in Map 2, highlighting so the strong connection between topography and the most apparent landscape traits considered for the preliminary assessment. Differences between the boundaries drawn by the two methods are not great and were very much expected due to the lack of precision of the visual inspection. The resemblance of the topographic domains and the distribution of main soil types over the area (Map 4) is also quite evident, supporting our tenet that the selected terrain traits are good indicators of soil-forming processes at the regional level. Representative topographic features for each TD are presented in Figure 1, while Figure 2 summarizes the composition of regional soil types within the TDs.

Also in agreement with our conceptual model, we observed the prevalence of rather old Oxisols (*Latossolos* after the Brazilian Soil Classification System – BSCS: Embrapa, 1999; correspondence between BSCS and USDA Soil Taxonomy classes after EMBRAPA: http://www.cnps.embrapa.br/sibcs/index.html), dystrophic Inceptisols and Ultisols (*Cambissolos* and *Nitossolos*, after the BSCS) in the topographic domains of the tablelands (TD4 to TD7). Notwithstanding the obvious commonalities, Map 3 subsumes into the tablelands a much wider extent than predicted initially, given the inclusion in TD6 of an important area dominated by a mosaic of very shallow Entisols (*Neossolos*, after the BSCS), young eutrophic Molisols (*Chernossolos*, after the BSCS) and rather old, dystrophic Ultisols (*Nitossolos*, after the BSCS). Yet these later soil types are characteristic of the more rugged terrain of the Sierra domain (TD2), suggesting that TD6 is transitional between the flat topography on top of the plateau and the highly dissected Sierra. A somehow higher ruggedness for TD6 when compared with the other domains in the tablelands seems to sustain this opinion.

Regarding landscape units over the tablelands, the classification discriminated 10 land-use / vegetation classes shown in Map 5. Some of the classes are mixtures of different types of vegetation, as is the case of classes 1 (natural forest / agriculture), 3 (natural forest / forestry) and 8 (agriculture / natural forest), and reveal a fine-grained pattern usually associated with small and medium-size rural properties and/or somehow irregular topographies. Classes 2, 9 and 10 are pure stands of native vegetation: campos, natural forests and montane forests on steep slopes, respectively. The remaining classes, in turn, identify areas under agriculture in which crops may differ in terms of phenology (annual vs. deciduous perennial) and development (early to full-grown to fading winter crops), the later as given by dissimilar timings for sowing across the region and images of different dates composing the Landsat mosaic (Miranda, 2005).

Regarding the linkage between topography, soils and land-use, a survey along five transects (see Map 6) gave an image rather similar to that primarily proposed from the preliminary integrative exercise. In TD4 (Fig. 3a), agriculture and mosaics of natural forest / agriculture predominate over the rather acidic Oxisols and, secondarily, on Entisols and Ultisols. TD5 (Fig. 3b) shares a very similar pattern, which led us to subsume both into a unique landscape type, equivalent to the *Planalto das Missões* in Map 2. In TD6 (Fig. 3c) the pattern tends to resemble that of the preceding units but, as it proceeds from Oxisols to areas with prevalence of young soils (Entisols in mosaic with Molisols or Ultisols), the importance of forests and natural *campos* increases. In turn, in TD7 there are two obvious patterns. The first, broadly corresponding to that of the Vacaria tablelands in Map 2, links the widespread occurrence of Oxisols with agriculture and natural and semi-natural grasslands (*campos*), in a way that the more dominant are the Oxisols, the more extended the agriculture. The second pattern (the Cambará – Bom Jesus tablelands) establishes a connection between the acidic Inceptisols (*Cambissolos* after the BSCS) and the grasslands, with an escalating presence of natural forests and forestry as young soils become more common.

The classificatory exercise present us the broad design of the relationship of land-use / vegetation units, soils and topography, whose results take very much after those of the integrative assessment. In both cases there seems to be a consistent connection among old soils, in the most stable surfaces, and the subtropical grasslands, and among the grasslands in deeper soils and agriculture as the dominant replacement system. Under the same scheme, forests, mostly replaced by small-farm agriculture and forestry (particularly in the higher tablelands to the east), should become more important as the area of occurrence of new soils widens. In ways the picture emerging from the successive overlying of classifications (topographic domains, soils and landscape units) is rather fuzzy. For instance, if one disregards the overall information from the transects on each particular topographic domain and focuses on the frequency of soil types in a specific land-use, for some transects natural forests seem to be largely located on latossolic soils. Whether these contradictory results are the product of the broad regional spatial scale of the soil classification (1:750,000: BRASIL 1973) in contrast with the more constrained coverage and higher resolution of the land-use classification (proximate scale 1:100,000), or the outcome of having left out some other important elements of analysis, is yet unclear. Zooming up on each area should be of help to disentangle the puzzling phenomena.

Spatial patterning at the local scale: the linkage between soil, land-forming processes and plant-cover

In the Santo Angelo area (28°10’ S, 54°20’ W, 200 m asl), Oxisols cover about 80% of the tablelands and lie over a quite thick weathering mantle (Streck 1992). In the corresponding Landsat composite (Map 7a), the Oxisols domain is marked by a coarse-grain pattern in which intense green tones (actively growing winter crops) dominate over slight red (bare soil), and yellowish tones identify the few remaining areas under *campo*. According to Streck (1992), other soil types, like the *Dystrudepts* (dystrophic Inceptisols evolving under humid conditions) and the *Argiaquolls* (eutrophic soils of the Mollisols class, with argilic horizons and evolving under per-humid regimes), are shallow soils in the more deeply eroded slopes: the Inceptisols over denuded basalt and the Mollisols on colluvial deposits.

While Mollisols have a negligible relative extension and can hardly be noticed in the Landsat image, the *Dystrudepts* form an intermediate fringe between the Oxisols and the soils of the bottomlands. By the beginning of the 90s they were mainly covered by semideciduous forests (Streck 1992), but by the time of the Landsat image (winter season of 2001) much of their area had already been converted into croplands. Young humic gleys (*Fluvaquents*) characterize the network of ill-drained bottomlands, which here is more extensive than in the Vacaria area and much more extensive than in the Cambará area. The *Fluvaquents* domain, in the image, is marked by a fine-grained texture in which plough soils appear as slight red, dark green identify areas under semideciduous gallery forest, and violet and brown are, respectively, flooded areas and grassy marshes.

The classification performed on the Landsat bands indicates for the area of Santo Angelo the land-use distribution shown in Map 7 (panel b). Mean topographic traits for the classes appear in Figure 4. For most traits, within-class variability was more important than the differences between land-use classes, which makes quite difficult to extract associated topographic patterns. This notwithstanding, the ranges of variability of relative altitude varied notably among the classes. In close agreement with the analysis of patterns in the paragraph above, forest remnants dominate in the lowest positions of the toposequences, where ruggedness and slope tend to be higher (characteristic of young soils). In similar conditions we found patches of forestry and shrublands, suggesting the expansion of forest plantations over former areas of semideciduous forest and the connection of shrublands to deforestation. Agriculture dominates at highest relative altitudes, where slope and ruggedness seems to be the lowest (characteristic of the areas of occurrence of Oxisols), while the subtropical grasslands are scattered in intermediate positions, forming isolated fringes around the agricultural fields or small patches in ill-drained areas associated with riparian forests.

A different pattern is found about 350 km further to the east. According to Potter (1977), in the Vacaria Experimental Station (28°33’ S, 50 °42’ W, 900 m asl) Oxisols evolved under a per-humid regime (*Haploperox*) and lie over the weathering mantle, occupying the upper and almost flat plateau and extending over ca. 50% of the area. In the Landsat composite (Map 8a), Oxisols appear marked by variable tones of red (bare soil or leafless perennial crops) to full green (actively growing annual crops), or by light brown when still covered by *campos*. Young soils of the Entisols order develop on isolated rocky crests and ridges, where erosion has washed out the regolith and the former soil as well; they make barely the five percent of the area, so they merge in the image with the surrounding soils and appear uniformly covered by *campos*, coinciding with Potter's (1977) observations in the Vacaria Experimental Station.

This notwithstanding, our field observations evidenced that these lithic Entisols are associated with a very shrubby version of the subtropical grasslands (*campo sujo*) and eventually with small groves. On steeper, middle and lower slopes, mostly covered by colluvia, rather old acidic soils of the Ultisols order have been reported and characterized by 1- an organic matter enriched topsoil and 2- a slight (if some) clay concentration gradient throughout the profile (*Palehumults*) (Potter, 1977). A forest-dominated mosaic of montane forests and campos covered the domain of the Ultisols, at least in the Vacaria Experimental Station, by the end of the 1970s (Potter 1977). However, in the Landsat image (Map 8a) they appear under herbaceous vegetation (annual crops and fallows). Moderately young soils of the Inceptisols order (evolving under per-humid to moist regimes over seasonally waterlogged bottomlands and exhibiting an organic matter-enriched topsoil –*Humaquepts*: according to Potter, 1977) are covered mostly by montane forests and grassy marshes.

According to the classification on the Landsat bands, land-use over the area is distributed as shown in Map 8b. Regarding topographic traits, within-class variability surpasses in all cases differences between classes (Fig. 5). Yet, notoriously distinct is the unit corresponding to riparian forests, located at the lowest positions of the toposequences where ruggedness and slope are greatest. Grassy wetlands also occupy the bottomlands, as expected, yet on smoother surfaces. Both observations suggest the association of riparian forests with the more recent soils on areas of intense drainage incision. Conversely, the units of grasslands do not differ much from the agricultural units, supporting so our tenet that agriculture have mostly expanded over natural grasslands.

Oxisols do not occur toward the eastern part of the plateau, above an altitude of ca. 1,000 m asl (e.g. the Cambará – Tainhas tablelands in Map 2) and dystrophic Inceptisols (*Dystrudepts*) become instead the most extended soil type (FIBGE 1986). The spatial domain of the *Dystrudepts* appears yellowish-brown colored in the Landsat composite of the Cambará / Tainhas tablelands (Map 9a), mostly under *campos* and semi-natural pastures. The It should be noticed the occurrence of extensive grassy marshes in the area. These marshes, however, seem not to be associated with the drainage systems, as it would be the case if they were the result of drainage infilling, but to be the consequence of a tectonically-produced overall pattern of uplifted and depressed blocks. This pattern is rather evident at fine scales, as can be seen in the RGB composite, or at the coarse regional scale.

The application of the ISOCLUST routine on the Landsat bands rendered, for the window corresponding to the area of Cambará, the distribution of land-uses shown in Map 9b. The units differed in terms of the topographic traits as shown in Figure 6. As in Santo Angelo and Vacaria, the comparison of the means suggest a pattern consistent with our preliminary assessment, with forests (either natural or cultivated) dominating over the more rugged lands of the eastern edge of the plateau, in spite of the overall prevalence of riparian and montane forests on the lowest positions of local toposequences. Yet within-class variability largely exceeded the differences among classes, making the above-mentioned pattern rather blur.

DISCUSSION

The geological and climatic setting of the regional landscapes

For all purposes related to our aims, the geological history of the Southern Brazilian plateaus starts in Jurassic-Cretaceous times, when several massive outpourings of effusive rocks built a deep volcanic mantle, The Serra Geral Formation, characteristic of the Paraná Geologic Province. The Serra Geral continental flood basalt is associated with the Jurassic-Cretaceous breakup of Gondwanaland and the transition of oceanic to continental magmatism, during the opening of the South Atlantic Ocean (South Atlantian event: Allauoa et al., 2002). The effusive field shows a composition continuum from basalt, to basaltic andesite, andesite, rhyodacite, and rhyolite (Fodor et al., 1985) and it extends over more than one million square kilometers, from central Brazil in Mato Grosso do Sul, to Rio Grande do Sul State (RS), north-western Uruguay, the north-eastern extreme of Argentina and eastern Paraguay.

According to Allaoua et al., (2002) during the transition from Cretaceous to Tertiary important tough more localized and isolated alkaline magmatic events took place (particularly in Southeast Brazil) followed by a ca. 5000 m vertical displacement in the adjacent oceanic margins. These processes set the current configuration of raised plateaus, continental rifts and shifting blocks of the Brazilian Atlantic shore. After the extended stability of the Miocene and lower Pliocene, the current stress regime settle in causing a much more active crustal uplift and the reactivation of ancient continental faults (the Cenozoic tectonics). Riccomini & Assumpção (1999) pointed at the remarkable influence of Cenozoic tectonics on the dynamics and topography of the Brazilian passive margin, summarizing the several traces of seismic and uplifting activity in all the main Brazilian geological domains. Such an activity could have been as recent as the Holocene in the Paraná geological province (see, for instance, Fernandes & Amaral, 2002). In our study area, evidences of Cenozoic tectonics could be the almost vertical scarps bordering the plateau, particularly to the east, the plateau's structure of grabens and horsts delimited by clean fault-related cleavages, very active process of denudation in the highlands during the Quaternary and the strong alignment of the surface drainage system. A similar set of terrain features have been described as indicators of Cenozoic tectonics in Southeast and Northeast Brazil (Uchôa de Lima, 2000).

During the South Atlantian magmatism, short events of eolian sand deposition formed sandstone strata interspersed with the effusive structures; however, these sandstone belts are rather uncommon in eastern Rio Grande do Sul, being more conspicuous in the Brazilian States of Paraná, Mato Grosso do Sul and to the west and north-west of RS. Basalts are the most widespread rock type, with acid effusives (mostly andesites and rhyodacites) appearing at the top of the plateau, mainly at the eastern fringe (FIBGE 1986). Given that from the end of the lava outpourings the whole landscape remained emerged, the area almost totally lacks overlaying sedimentary formations; there were, however, some areas of active continental deposition during the Tertiary (the sandstones of the *Tupanciretã* Formation) whose remnants outcrop toward the west of the study area (FIBGE 1986, 1990).

The foregoing sheds light on a large-scale dynamics, active until recently, that determined macro and meso-scale topographic patterns. In our study area, it uplifted the effusive mantle to its actual elevation and formed a cuesta-like surface, smoothly tilting to the west but falling almost vertically to the coastal plain in the eastern border (Figure 7, transect A). Two main rivers flow westwards: the *Pelotas* and *das Antas* rivers, deeply dissecting and dividing the plateau. Other watercourses belonging to these basins, like the *Carreiro*, the *Guaporu*, the *Telhas* and the *Pirabucu* rivers, have completely dissected the tablelands from north to south. As a result, the plateau is now partitioned into three large units. The largest one is known as *Planalto das Missões*, extending eastwards from the Uruguay valley to ca. 52° W. There, a fringe of broken relief separates the *Planalto das Missões* from the *Planalto das Araucarias*. The later, in turn, has been divided by *das Antas* river into the Vacaria-Bom Jesus and the Cambará-Tainhas tablelands, with a Sierra relief, originally covered by forests, lying in between. (Figure 7, transect B). Besides the major fault scarps (mainly related to the Pelotas faulting system: see Allaoua et al., 2002), the tablelands exhibit a dense system of faults and fractures with two main directions, one ESE – WNW and another almost perpendicular to it (FIBGE 1986, 1990). In summary, long-term tectonics determined two major types of landscape domains in the basaltic area of Rio Grande do Sul State: the *Sierra* domain, covering the scarps and most dissected areas of the plateau, and the tablelands domain, which lie atop.

The current relief of the tablelands is an almost level pediplain modeled, all along the Tertiary and the Quaternary, by several successive pediplanation processes. These resulted in a gently undulating surface, denuded and reworked by erosion (FIBGE 1986). As a consequence of the structural control over the geomorphic modeling, a coarse-grained landscape emerged, with fairly flat tops and scatter mammillary hills, divided by a rectangular drainage system. Strictly controlled by a quite dense system of crossing faults, the plateau topography abounds with rocky ridges, hills and abrupt scarps (some of them up to one hundred meters high towards the east of the plateau).

Referring to the actual climates, the study region may be considered as a wide ecotone between the tropical climates of southeastern Brazil and the temperate climates of Southern Rio Grande do Sul and Uruguay. This subtropical belt, with average thermal amplitude (mean temperature difference between the coldest and warmest months) of 8° to 10°C, is in fact transitional between the constant monthly temperatures that characterize tropical climates, and the fairly contrasted seasonal regime of the warm temperate zone. As there is a significant altitudinal gradient of about 1000 m asl, mean annual temperatures range from 20° to 14°C; the mean number of frost days increases accordingly from 10 per year, in the western, lower border, to more than 30 days on the eastern highlands (FIBGE 1990). The whole region has a humid climate, with an eastward (seaward) precipitation gradient from above 1700 to 2300 mm yr.

Although rainfall is fairly well distributed along the annual cycle, the analysis of long-term rainfall and temperature records suggests that the high interannual variability of this parameter, distinctive of subtropical regions (Figure 8), may lead to periods of slight to severe water deficit. Similar conclusions were attained by Buriol *et al.* (1979). These variations are reinforced in the region by the *El Niño – La Niña* oscillations, being La Niña years characterized by below-the-mean total rainfall (Jacobsen *et al.*, 2003). In spite of the rather recent current climatic setting, perhaps characteristic of the last 3,000 years, there is an apparent connection between its major drivers (temperature and rainfall) and the patterning produced by tectonics, on determining the overall distribution of the main natural vegetation types. Within the *Sierra* spatial domain, forest physiognomies prevail. Tropical Atlantic rain forests extend over the seaward side of the plateau scarps, where relatively warm oceanic waters maintain humid, tropical conditions down to 30°S. *Araucaria*-dominated forests (montane forests) are characteristic of the highest fringe of the sierras, occupying the wettest and foggiest parts of the study area, while semideciduous forests increasingly dominate westward, where continentality determines larger differences between the coldest and the warmest months, as well as between the wettest and the driest seasons (Pillar and Quadros 1997, FIBGE 1986, Klein 1975). The entire area presents a distinctive pattern of land-use and human occupation, with small to medium size agricultural farms extending along the valleys, and forest plantations (*Pinus* spp. and *Eucalyptus* spp.) encroaching over a matrix of natural forests in the Sierra slopes.

Differently, in the tablelands domain a mosaic of two contrasting vegetation physiognomies, subtropical grasslands (*campos*) and forests, constitutes the natural vegetation. To this mosaic motif, recent land-use dynamics has superimposed a coarse-grained pattern in which croplands, forest plantations and managed pastures replace, to a variable degree, the original ecosystems. Although in the Sierra domain the relation between climate and different types of natural forests is evident, on the tablelands main climatic parameters do not seem to account for the distribution of either major natural physiognomic type. Nevertheless palynological data suggest that forests have expanded to a greater extent over the higher (colder and more humid) tablelands to the east, than over the low tablelands to the west (see Behling et al., 2004; Behling et al., 2005).

Soil, geomorphic units and vegetation

Highly weathered, acid Oxisols (*Latossolos* after the BSCS) cover most of the study area, followed in importance by dystrophic Ultisols (*Nitossolos and Argissolos*), Inceptisols (*Cambissolos*) and Entisols (*Neossolos*), while eutrophic and mesotrophic types like Mollisols (*Chernossolos*) and Alfisols (*Planossolos* and *Solos Hidromórficos*), are less common. Oxisols without distinctive features other than the oxic horizon, *Hapludox*, cover most of the tablelands wherever a deep weathering mantle still persists. They seem to have evolved almost exclusively on basalt (being almost absent on acid effusive rocks), but occur over a wide range of altitudes, from the lowest western border of our area, below 100 m asl, to an upper limit of 1,000 m asl, where they are replaced by Inceptisols, as dominant class, over the acid effusives extending at higher altitudes further to the east.

Basalt is a microcrystalline, silica-poor and quartz-deprived rock on which uniformly clayey soils develop. Notwithstanding this consistent trait of their parent material, several classes of *Hapludox* are recognizable on the plateau, according to their position in the altitudinal gradient and their soil water regime. For instance, a yellowish goethite enrichment characterizes Oxisols in lower positions along toposequences, under wetter environments favored by subsurface downhill water movement, while reddish, hematite enriched soils are characteristic of higher, best drained sites (Curi and Franzmeier 1984). Likewise, the altitudinal gradient is positively related to the organic matter enrichment of the topsoil (see FIBGE 1986). In soil catenas throughout the Oxisol-dominated area, these highly weathered soils always occupy the rather flat top of the tablelands and the upper part of the slopes, exception made of the residual rocky hills and crests which are topped with lithic Entisols. Other types (Ultisols, Alfisols, Mollisols and Inceptisols) in turn, predominate on the relatively steeper hill slopes and over the bottomlands. The description of typical soil mosaics in the Santo Angelo and Vacaria tablelands exemplify this pattern.

Several physical and chemical characteristics of the Oxisols surely are important vegetation drivers, both in the Vacaria and the Santo Angelo tablelands. Firstly, their depth, good drainage conditions and clay texture assure significant water storage at field capacity, preventing both pronounced water deficit or water saturation respectively in drier or wetter years. Secondly, they are highly dystrophic as may be inferred from the very low figures of exchangeable bases, their negligible available P, and high Al^{2+} CEC saturation (Table 1). The almost complete lack of primary minerals in the profile and the usual several meters deep weathering front, complete the scenario of nutrient constraint. In contrast, Entisols are quite shallow, about 20 to 50 cm, and correspond in fact to 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, and when they occur over sediment-filled valleys, where the seeping rainwater accumulates, they develop an organic carbon-enriched A_1 horizon (characteristic of the *Fluvaquents*) being either covered by gallery forests or by grassy wetlands. It is to be noticed that as the drainage system develops, forest frequency increases in the bottomlands.

Soil distributional patterns in areas dominated by Ultisols and Entisols (namely the Cambará / Tainhas tablelands) are remarkably different. Besides occurring on the middle and lower hill slopes of the more dissected areas of the tablelands, Ultisols are the typical soil unit on the Sierra slopes. In both cases, they are neither as deep as the Oxisols nor show the oxisol-characteristic thick alterite mantle. Although Ultisols seem to have evolved where the landscape was rejuvenated by erosion, these have undergone intense leaching as we infer from their extremely low base saturation (Ca^{2+}, Mg^{2+}, K^{+}) and assimilable P amounts (see Table 1). This notwithstanding, their relatively shallow weathering front may neutralize nutrient constraints to deep-rooted vegetation as suggested by the relative dominance of forests vegetation developing on them.

Developed over acid volcanic rocks (rhyodacites and rhyolites), most often on hill slopes with a thin cover of colluvial material, *Dystrudepts*, in spite of their young age, seem to be more dystrophic than the Oxisols of the lower tablelands. For instance, they exhibit a rather high CEC but very low exchangeable bases (Table 1). However, the A_1 horizon has the highest organic matter content of any other soil in the whole area, probably due to its long and uninterrupted evolution under grassland vegetation. The apparent contradiction between young age and degree of desaturation may be understood considering the colluvial material in which they evolve. Landscape evolution suggests that this material has been thoroughly weathered in previous soil-forming cycles, being already depleted of primary minerals before its accumulation on the hill slopes. If so, *Dystrudepts* develop from inherited kaolinitic clays, Fe and Al sesquioxides. In some places dystrophic Inceptisols do not occur over colluvial deposits; there, they 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.

In spite of the prevalence of highly dystrophic, polycyclic soils all over the three landscape types over the plateau, they sharply differ in terms of frequency of the different soil types: the fact Oxisols are much more extended in Santo Angelo than in the Vacaria area (notwithstanding their similar parent material), while very acidic Ultisols and *Dystrudepts* are important only in the higher tablelands, seems to point at significantly different environmental conditions controlling soil evolution throughout the last millennia. When comparing the areas of Vacaria (900 m asl) and Cambará/Tainhas (1000 m asl), the lack of Oxisols in the later may also be a consequence of lithological differences: basic effusives in Vacaria and acid effusives in Cambará/Tainhas, though Oxisols also evolved over the relatively acid, sedimentary rocks of Lages, a few kilometers further to the north at ca. 800 m asl (Almeida *et al.*, 2000). Another interesting fact regards differences in the extension of *Argiaquolls* and *Fluvaquents*, which find their maximal expression in the Santo Angelo area but are either absent or poorly represented in the Cambará/Tainhas and Vacaria tablelands.

The general picture

Our analysis has illuminated the patterns of spatial association between vegetation, landforms, land-use and soils. It was shown that soils and landforms are responsive to the geological, climatic and geomorphic setting. Considering the coexistence of grasslands and forests throughout the study area, it is worth noticing that the post-Columbian dynamics of human occupation and land use has obscured to some extent the influence of soil features on shaping the spatial pattern of natural vegetation mosaics. Nevertheless, it is clear that, in the three landscape units, the *campos* tend to occupy the rather old, acidic soils on the relict surfaces of the pediplain, while forest vegetation increasingly predominates on areas whose soil profile have been rejuvenated either by surface stripping, dissection or aggradation. Whether this observation has anything to do with primary minerals or nutrient availability in the soil profile remains uncertain. In Figure 9 we present an idealized model of forest – grasslands distribution, in the three landscape-types identified over the basaltic tablelands of north Rio Grande do Sul.

The widely accepted interpretation considers upland *campos* to be remnants of a colder and drier steppe climate that would have come about during the Late Pleistocene and Early Holocene (Schultz 1957, Klein 1975, Bigarella and Andrade-Lima 1982, Waechter et al. 1984, Pillar and Quadros 1997, Pillar 2003, Behling et al. 2001, Behling et al. 2004, Behling et al. 2005, 2007). Under the current wet subtropical regime, forests are considered the climatic vegetation, forests and grasslands distribution is thought to be transient and the mosaicked pattern, an intermediate stage on the regional landscape evolution towards the novel climatic equilibrium. According to this scenario, current landscape patterns are the result of the ongoing, as it is yet incomplete, process of one major physiognomic type (forests) advancing over the other (*campos*). Behling *et al.* (2004, 2005, 2007) have hypothesized that such a process has been controlled by grassland fires since early in the process of forest expansion, though cattle trampling and grazing became an important additional driver from the 17-18th centuries on (Goulart 1978). More recently, cattle grazing intensified by means of an increased frequency of prescribed fires and the introduction of exotic forages. This along with land conversion into agriculture and forestry, may have halted forest expansion and determined the sharp boundaries nowadays observed between patches of contrasting vegetation types.

If these disturbances were, however, eliminated forests could be expected to expand over the entire region following two different paths: 1- by forming isolated tree pockets, when tree seedlings find an appropriate environment to grow, then facilitating the establishment of further forest elements under their canopy (further details about the subject in Duarte et al. 2006); 2- by shading and out-competing the grasses in the forest – grassland boundaries, whose space would be then taken over by tree seedlings. The net outcome would be the gradual overgrowth of the forest area at the expense of the grassland (see Oliveira & Pillar 2004). The key questions at this point are: to what extent is this conceptual model of forest expansion compatible with the idealized profiles of vegetation distribution resulting from spatial-pattern analysis? And if so, how can soil-forming and land-forming processes be included as additional drivers of the processes behind forest expansion? These questions aim at assessing whether forest expansion is equally probable under any of the environmental circumstances determined by the regional setting, land-use and land-use changes put aside.

At the general level of this work, the picture drawn so far of forest and grassland distribution over landforms and soil units, seemingly supports the model in which fire-related disturbance regulates forest expansion. According to Pillar (2003), three different set of variables are of importance for that model. The first set is of biotic nature and refers to interspecific interactions of competition, facilitation and dispersion, all of which make up the mechanism behind forest settling and expansion. The second set is of geographic nature and refers to the proximity of forest-seed sources. The third set refers to the suitability of the environment for the establishment of forest elements. Being fire disturbance the leading force modulating the rate at which the forest advances over the grassland matrix, the environmental factors important to determine a 'suitable' site should be very influential on the frequency and intensity of burning events. Pillar (2003) identified soil depth and rockiness as being two of these meaningful environmental factors, taking into account that the productivity of the grassland decreases over shallow, rocky soils. Shallowness and rockiness are quite probable soil characteristics on the topographies already described as being typical of forests. If we consider several situations in which dispersal agents have brought the seeds that would grow to develop a new forest pocket, only in those scenarios of diminished grassland productivity are burning events expected to be less frequent and/or intense and the survival of forest seedlings favored.

This observation calls attention to the factors of the physical environment that would abate the carbon balance of the grasslands, and to how these may relate to geomorphic and soil forming processes. Nevertheless, if soil rockiness and shallowness act indeed as strains on grassland productivity to the point of affecting fire probability, the reasons are not obvious. According to Jacóbsen *et al.* (2003), during the drier La Niña years NDVI yearly-averages of pixels largely occupied by *campos* experienced a stronger drop of carbon assimilation when compared with other vegetation types. This suggests a relatively higher sensitiveness of the campos to water deficit. Being shallow and rocky soils those with the least water holding capacity, water availability seems to be a good way to downscale from regional soils and landforms patterns to grasslands productivity and thence to local dynamics of forest / grassland accretion. This notwithstanding, it is important to consider that the climate in the whole region is as humid as to make water deficiency a minor constrain to the carbon balance of the grasslands. This holds true particularly well for the eastern tablelands, where forests experienced the most considerable expansion during the last millennia (see Behling *et al.* 2004 and 2005). It is therefore necessary to evaluate regional patterns of grassland productivity and relate them with the several soil conditions in which these occur, in order to determine whether temporary soil water deficits are forceful controls of biomass accumulation and then on fire frequency and intensity.

Some other doubtful points emerge when we consider the whole spectrum of environmental situations in which forests and grasslands coexist. The fact that deep lateritic soils are clearly dominated by *campos* while shallow regolithic soils are so by forests, suggests some influential role of the availability of primary minerals on the suitability of the forests to take over the space. This is to say that it is also essential to appraise forest productivity under different environmental conditions, at a regional level, to see whether there exists some forest-productivity threshold below which forest wouldn't succeed colonizing the grasslands, even in a scenario of receding fire frequency. Needless to say that such a threshold, if any, should be specific of each forest type.

Other questions regard the soil units and landforms in which both vegetation types occur, as it happens on the hydromorphic units in the bottomlands and on the Ultisols associated with colluvial slopes. In the first case, we aim at identifying the mechanisms conducive to the expansion of gallery forests over the grassy marshes in the waterlogged bottomlands. In the environment of the grassy marshes burning events have the least frequency, coming about only during the drier years. However, these events may attain great intensities, depending on the dryness reached by the characteristic clayey soils and on the accumulated standing dead biomass. An effective environmental control on fire disturbance, in this relatively fertile and wet scenario, should then constrain fire propagation or the accumulation of standing dead in the herbaceous layer. The later should furthermore have little or no negative effect on the ability of forest seedlings to grow. Besides, it should also explain the preferential location of the forests along swift-flowing, instead of still-standing waters. A similar thinking may be applied to the forest – grassland mosaics on Ultisols.

It is widely accepted that some terrain features influence patterns of fire propagation, which in turn affects the likelihood of fire occurrence over the space. For instance, slope-induced convection forces the flaming front to move upwards instead of down the slope during a burning event (Viegas, 2004). This phenomenon makes the lowest positions of a landscape the least probable targets of fire expansion and would help to explain why we have observed a preferential location of forests in the lowest positions of local toposequences. Nevertheless, in the eastern tablelands patches of montane forest are frequently found on intermediate and elevated positions, right after the grassy marshes on the bottomlands or the *campos* on colluvial slopes (Photos 1 and 2). Whether this pattern is the product of deforestation is uncertain.

An additional mechanism may relate to landscape evolution. Given the little to moderate development of the drainage system over the tablelands, the expansion of the riparian forests throughout the last millennia seems to have been concomitant with the progressive formation of a surficial net of stream channels. This dynamics have certainly enforced the conversion of many of the local wetlands from low-energy basins to high-energy riverine systems (see Brinson & Lee, 1989 and Brinson, 1993, for further details on this classification for wetlands). According to Brinson (1993), main differences between both wetland classes concern hydroperiod and nutrient fluxes, in a way that low-energy basins are broadly characterized by large hydroperiods and slow nutrient fluxes while high-energy riverine wetlands display the opposite features. A decreasing hydroperiod leads to more frequent and stronger dry spells, whose effects are expected to be worse on shallow-rooted grassy vegetation developing on clayey soils. In turn, enhanced nutrient availability may have promoted forest development.

A similar geomorphic mechanism of forest expansion could also apply to those situations in which forest develops along ravines dissecting the colluvial slopes, or around mid-slope wellsprings. In the two cases concentrated erosion would provide grass-free sites for forest elements to takeover and the new hydrologic regime would supply nutrients otherwise scanty. Moreover, the enlarged lateral drainage of the surrounding soils could constrain the productivity of the grasslands developing on, either by an enhanced soil leaching or an increased probability of dry spells, relaxing so the fire-related disturbance regime over the wider area.

Further research is needed to test the validity of the proposed connection among fire disturbance, landscape evolution and ecosystem spatial patterning, but this task is neither obvious nor easy to carry out. We should certainly estimate the effect of highly dynamic land-forming processes on the productivity of grasslands and forests, in defiance of issues concerning the time scale of the geomorphic phenomena and the readiness of vegetation response that make a direct survey a very difficult endeavor. Instead, a regional comparative approach could provide a promising approach to the problem. Likewise, it is important to make predictions on the basis of this conceptual model, which would be later compared with a larger and independent set of observations along meaningful environmental gradients. Predictions can also refer to the expected outcome of long-term climatic change on terrain evolution and ecosystem patterning, which is to say that what we have concluded on the basis of spatial analysis should also hold true when analyzing patterns in time.

FINAL REMARKS

In this report we accomplished the recognition and description of main landscape types in the basaltic tablelands of Rio Grande do Sul, and proposed mechanisms and controls responsible for their characteristic patterns. From the spatial association of terrain features, soils, land-use and vegetation, we identified three basic landscape types and broadly defined their spatial domain: 1- the *Planalto das Missões*, 2- the *Vacaria* tablelands and 3- the *Cambará – Tainhas* tablelands. The *Planalto das Missões* type occupies the largest area on top the basaltic plateau and can be recognized by the overriding extension of deep and acidic soils of the Oxisol order, covered by cash-crop agriculture and sparse remnants of the subtropical grasslands (*campos*). Semideciduous forests prevail on the ill-drained depressions where richer soils of the Molisol and Entisol orders develop. These depressions are secondarily occupied by grassy marshes and small patches of forestry.

The second pattern corresponds to the Vacaria tablelands and is still dominated by agriculture developing on Oxisols, though some other units together make about 40 percent of the area. Oxisols also hold most of what remains of the subtropical *campos*. Natural forests exhibit a physiognomy closer to that of the highest areas of the plateau, richer in evergreen and mountainous elements, and appear forming a network of galleries, generally associated with grassy marshes, or as small isolated patches on the colluvial slopes. As in the previous landscape type, forests are largely associated with young soils of the Entisol order, yet on the colluvial slopes they form a mosaic motif with some of the remaining grasslands.

The *Cambará – Tainhas* tablelands almost lack Oxisols and agriculture is barely a marginal activity. Leading land-uses are silviculture and cattle raising on pastures and semi-natural grasslands. The most widespread soil type is a humic, quite dystrophic Inceptisol (Dystrudept), mostly developing on inherited kaolinitic material. Over this soil type natural and secondary grasslands dominate, though the striking advance of commercial forests may well soon change the entire physiognomy of the unit. Forest plantations and natural montane forests share the areas characterized by more rugged topographies, yet natural forests still prevail on the bottomlands along with grassy marshes. Forests may also occupy the rocky outcrops or form variable-sized groves on the colluvial slopes.

The picture so far described tells of a rather close relationship among the distribution of the major physiognomic types of the vegetation, soils, land-use and land-forming processes. In this picture, the grasslands prevail where terrain and soil features suggest there are the remnants of an old pediplanation surface. Forests, on the other hand, seems to dominate wherever geomorphic agents have rejuvenated the landscape, However, the fact is that in a realistic model for understanding the development of the forest-grassland pattern, fire disturbance cannot be ignored, for it has been present concomitant to the forest expansion process verified throughout the second half of the Holocene. It is then essential to correlate the fire-disturbance regime with the leading processes responsible of soil and terrain evolution.

The most promising way to correlate processes of such a different nature is through a functional approach to the vegetation. Ecosystem functioning is then the most appropriate manner to downscale from the regional realm where terrain and soil-forming phenomena dominate spatial differentiation, to the fine-scale processes at which biological factors are most influential in the production of patterns of spatial heterogeneity. Fire frequency and intensity have to be understood as functional attributes of the grasslands, emerging from the interaction of biological, soil, land-use and climatic drivers. Likewise, the impact of the fire regime on the ability of forests to expand need to be understood in relation with the functional attributes of the forests, as diverse as these can be, given the variety of physiognomies, phenologies and environmental situations in which they occur.

As we have seen, the problem identified as specific to Landscape Ecology, that is the emergence of patterns in the space of ecological variables (in this case, different types of vegetation and ecosystems), demands a broad scope than greatly exceeds the specific fields of the different ecological and environmental disciplines. Yet it establishes links among them, in order to establish the causation chains and governing principles behind the processes of spatial pattern formation. During the presentation, regional landscapes have been portrayed as organized arrangements of topographic units, landforms, land-uses, soil types and vegetation types. However, these concepts have been used sequentially in the context of a hierarchical scaling-ladder in which, what sets the ground to define what and how a landscape is, is a matter of recognizing the main processes producing spatial heterogeneity at each hierarchical level.

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Table 1. Characteristics of some soil profiles in the study area, after FIBGE (1986) and Streck (1992). Numbers separated by a virgule (/) correspond to the A1 / B2 horizons.

Tableland	Cambará/Tainhas		Vacaria			Santo Angelo	
Profile Nr[1]	22	20	19	18	16	5	5 (*)
USSS soil unit	Haplumbrept	Palehumult	Haplhumox	Umbrorthox	Paleudult[2]	Haplorthox	Argiudoll
Depth (cm)	68 / +180	30 / 320	55 / 190+	34 / 330+	10 / 320	40 / 120	20 / 86
Clay %	54 / 64	69 / 83	73 / 83	75 / 86	57 / 83	62 / 74	53 / 71
C %[3]	4.1	2.3	6.6	2.7	1.3	1.2	5
C / N	11	10	11	11	9	10	-
pH (water)	4.9 / 5.0	5.0 / 5.3	4.8 / 5.2	4.9 / 5.2	5.6 / 4.8	5.3 / 5.4	5.4 / 5.2
CEC meq/100 g clay[4]	24	15	13	15	18	7	21
S meq/100 g soil	2.7 / 0.4	3.1 / 0.7	5.6 / 0.8	3.5 / 0.8	8.1 / 5.2	3.1 / 1.7	11 / 15
V %	9 / 3	19 / 6	23 / 8	16 / 5	53 / 17	35 / 26	64 / 74
Al+++ %	23 / 51	22 / 39	11 / 25	20 / 44	1 / 51	26.65	1 / 3
Ki (Si02 / Al203)	1.9 / 1.8	1.9 / 1.9	1.8 / 1.7	2.0 / 1.8	2.2 / 2.6	2 / 1.9	-
P assimil. (ppm)	3 / 1	< 1 / < 1	2 / 1	2 / 1	4 / 1	2 / 1	7 / 8
P_2O_5 %	0.12 / 0.09	0.17 / 0.14	0.20 / 013	0.13 / 0.08	0.19 / 0.07	0.22 / 0.21	-
K+ meq/100 g soil	0.22 / 0.03	0.20 / 0.05	0.76 / 0.04	0.23 / 0.04	0.25 / 0.13	0.39 / 0.04	0.23 / 0.14

[1] Profile number in FIBGE 1986. (*): in Streck 1992.

[2] This soil in a fieldcrop has been limed, fertilized and plowed.

[3] In the A_1 soil horizon

[4] In the B_2 or the (B) soil horizon

Figure 1. Terrain descriptors of the first order landscapes (topographic domains). Mean ± SD. In the X axis: 1 + 2: Sierra domain, 3: Lowlands, 4 + 5: *Planalto das Missões*, 6: transitional between the *Planalto das Missões* and the Sierra, 7: *Planalto das Araucárias*.

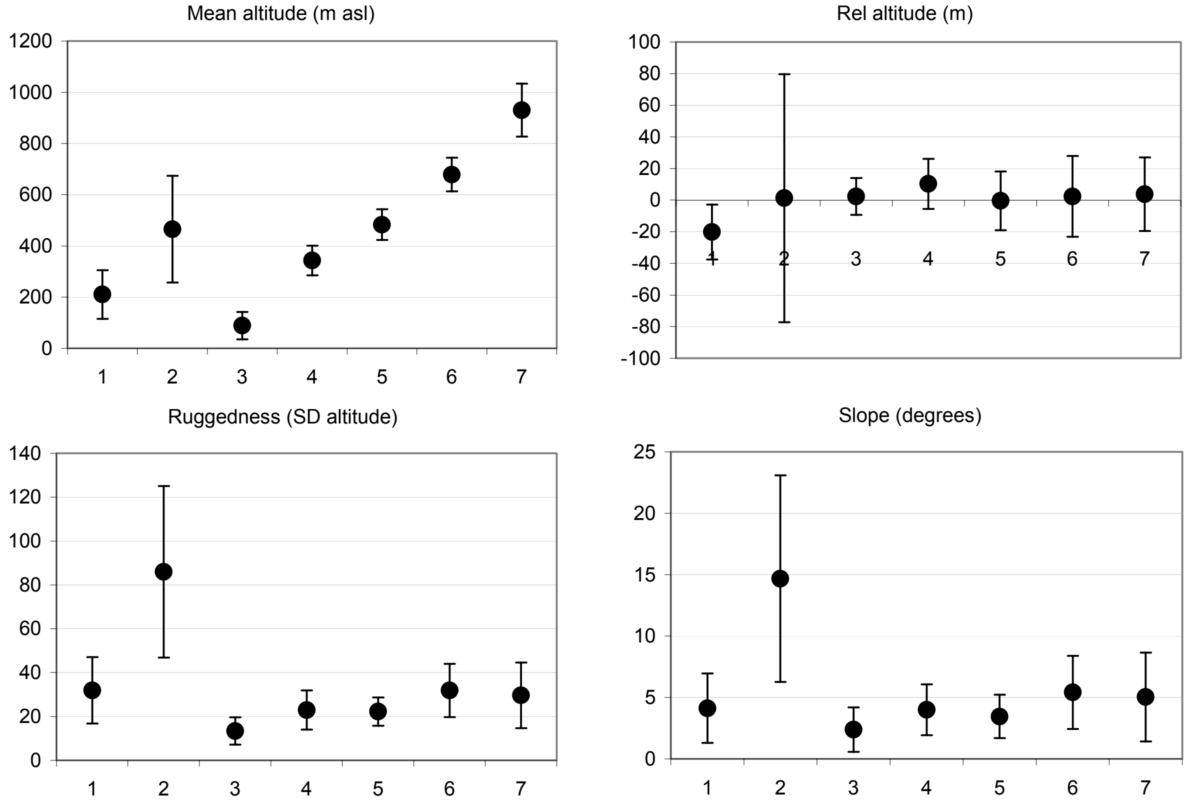


Figure 2. Soil types of the first order landscapes in the basaltic tablelands. Soil data from Streck *et al.*, 2002. In the X axis : TD1 - Sierra piedmont, TD2 - Sierra, TD3 - Lowlands, TD4 and TD5 - *Planalto das Missões*, TD6 - transitional between TD2 and TD5, TD7 - *Planalto das Araucárias*. Soil Types in legends : Neo – lithic Entisol, Vert – Vertisol, Ar/Ni – mosaic of Alfisols and Ultisols, Luv : Entisol of alluvial origin, Camb : Inceptisol, Neo/Ni – mosaic of lithic Entisols and Ultisols, Plan - hydromorphic soil in floodplains, Arg - Alfisol to Ultisol, Ch/Neo – mosaic of Molisols and lithic Entisols, Glei – hydromorphic soil with Gley horizon, Nito – Ultisol, Cher – Molisol, Lato – Oxisol.

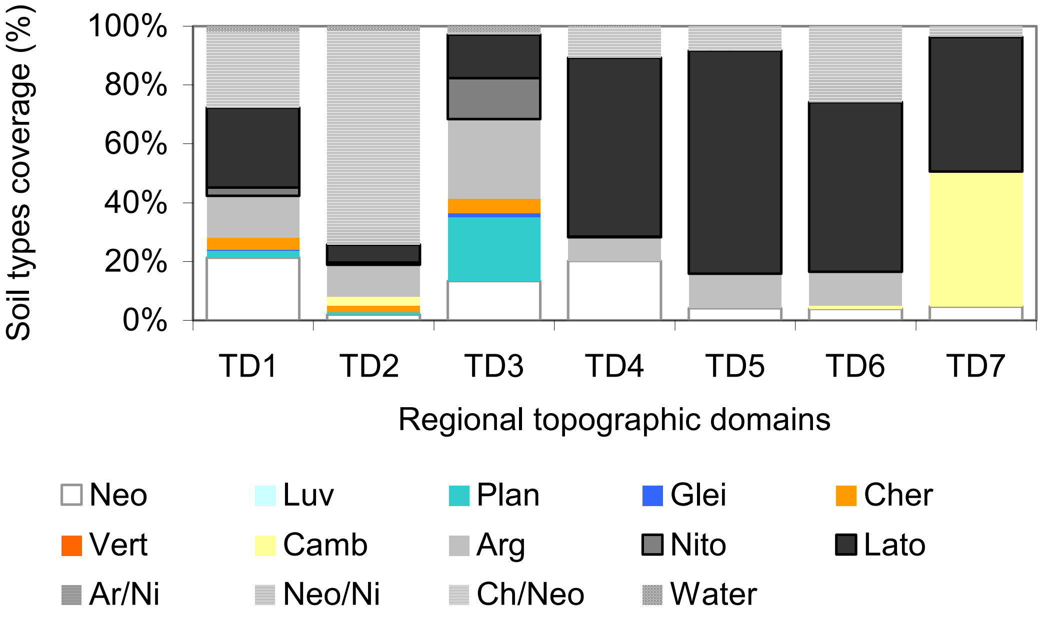


Figure 3. Land-units frequency (Y axis) as number of pixels per soil type in the topographic domains of the tablelands (TD4 to TD7). Figures 5a, b, c, d, and e refer to transects A, B, C, D, and E respectively. Soil type legends as in Figure 4. Land-units in the X axis: NF/Ag – mosaic of natural forest/ agriculture, Ca – campos, NF/Fo – mosaic of natural forest / Forestry, Ag – agriculture, Ag/NF – mosaic of agriculture and natural forest, NF – natural forest. Topographic domain and its corresponding coverage (%) over the transect in the graphic box

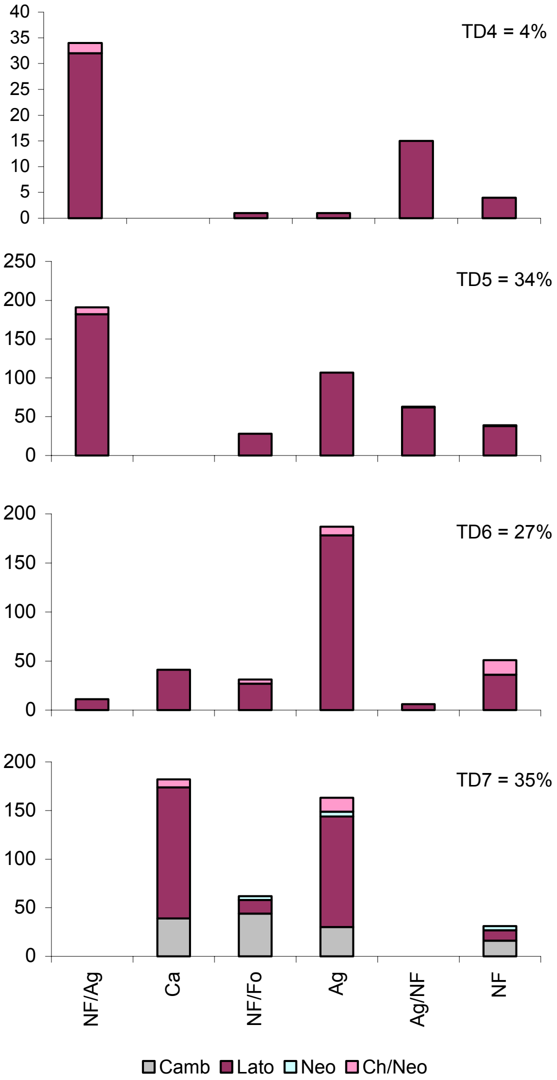


Fig. 5a.

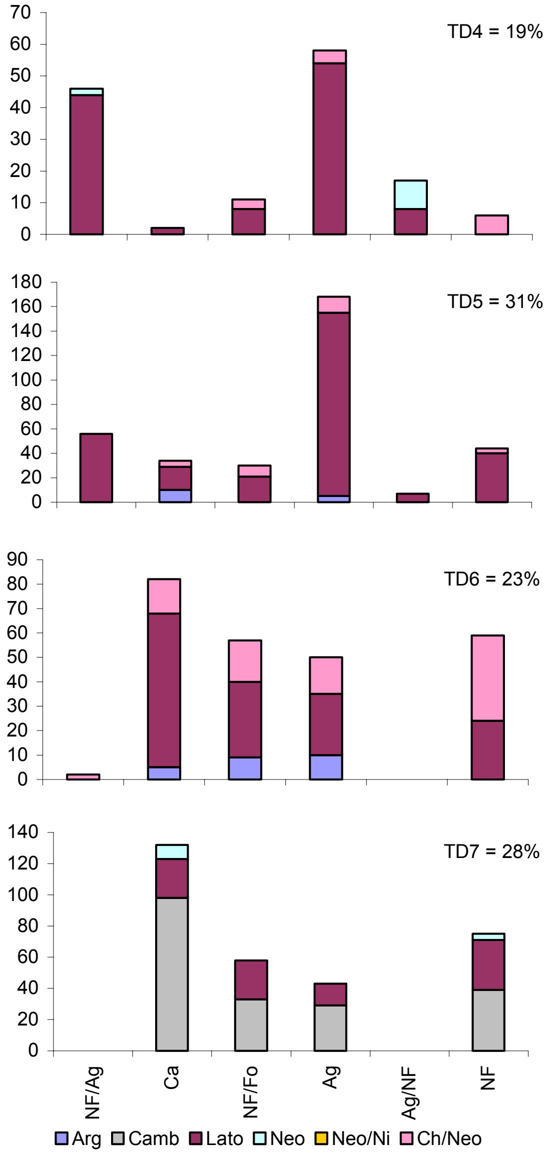

TD4 = 19%
0
10
20
30
40
50
60
70
TD5 = 31%
0
20
40
60
80
100
120
140
160
180
TD6 = 23%
0
10
20
30
40
50
60
70
80
90
TD7 = 28%
0
20
40
60
80
100
120
140
NF/Ag
Ca
NF/Fo
Ag
Ag/NF
NF
Arg
Camb
Lato
Neo
Neo/Ni
Ch/Neo

Fig. 5b.

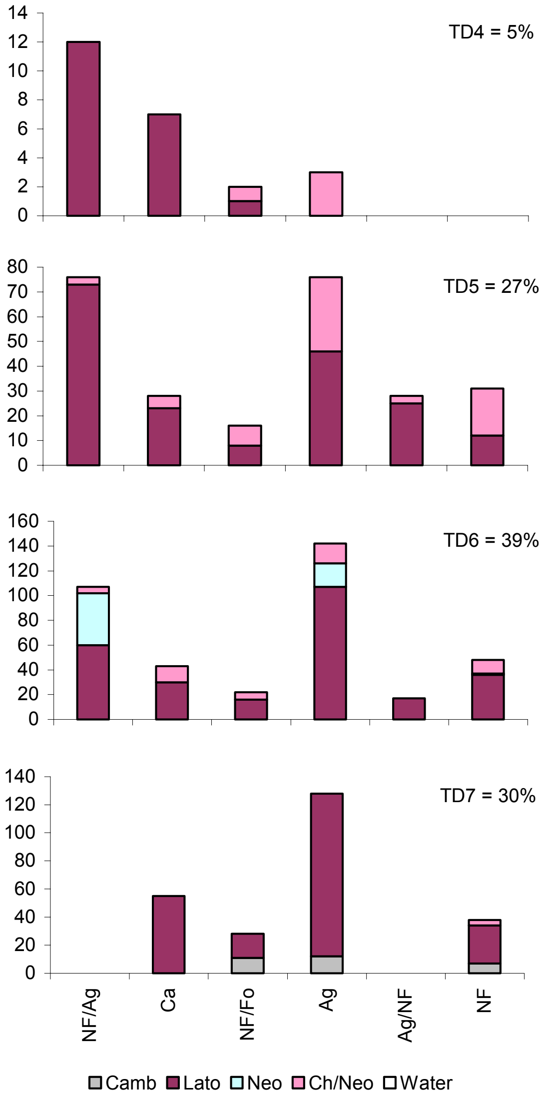

14
12
10
8
6
4
2
0
TD4 = 5%
80
70
60
50
40
30
20
10
0
TD5 = 27%
160
140
120
100
80
60
40
20
0
TD6 = 39%
140
120
100
80
60
40
20
0
TD7 = 30%
NF/Ag
Ca
NF/Fo
Ag
Ag/NF
NF
Camb
Lato
Neo
Ch/Neo
Water

Fig. 5c.

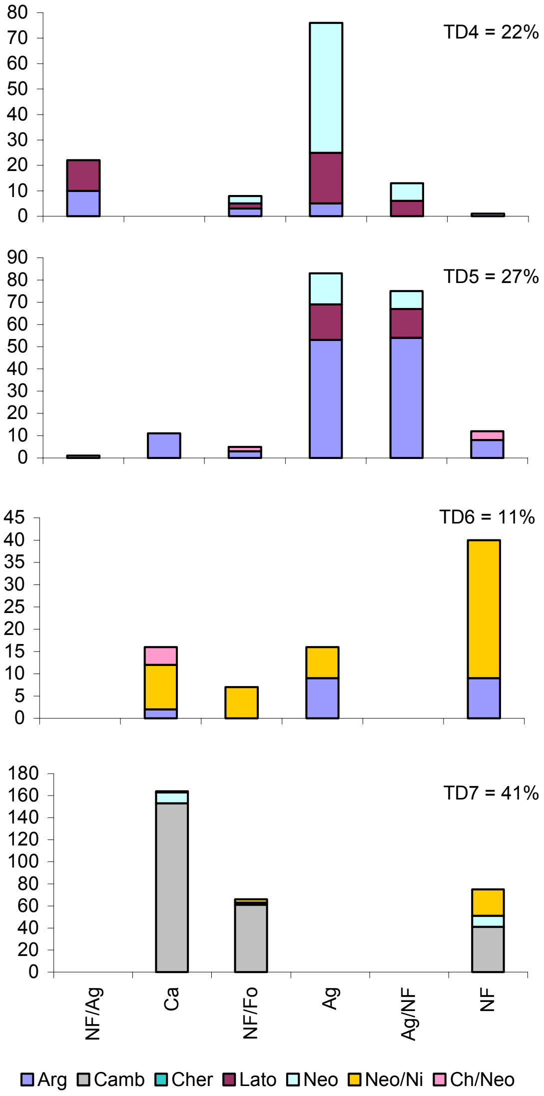

TD4 = 22%
TD5 = 27%
TD6 = 11%
TD7 = 41%
0
10
20
30
40
50
60
70
80
90
0
5
10
15
20
25
30
35
40
45
0
20
40
60
80
100
120
140
160
180
NF/Ag
Ca
NF/Fo
Ag
Ag/NF
NF
Arg
Camb
Cher
Lato
Neo
Neo/Ni
Ch/Neo

Fig. 5d.

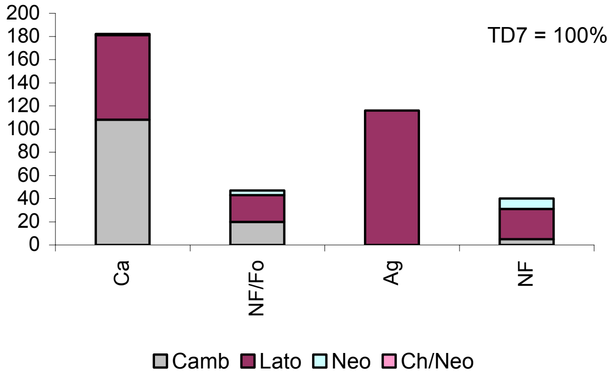

TD7 = 100%
0
20
40
60
80
100
120
140
160
180
200
Ca
NF/Fo
Ag
NF
Camb
Lato
Neo
Ch/Neo

Fig. 5e.

Figure 4. Terrain characteristics of the land-units in Santo Angelo: mean ± SD. Land-units in the X axis: RF – riparian forest, Gs – campo, Ag – agriculture, Ft – Forestry, FS – mosaic of forest / shrubland, Sh – shrubland, GW – grassy marsh, MF – montane forest.

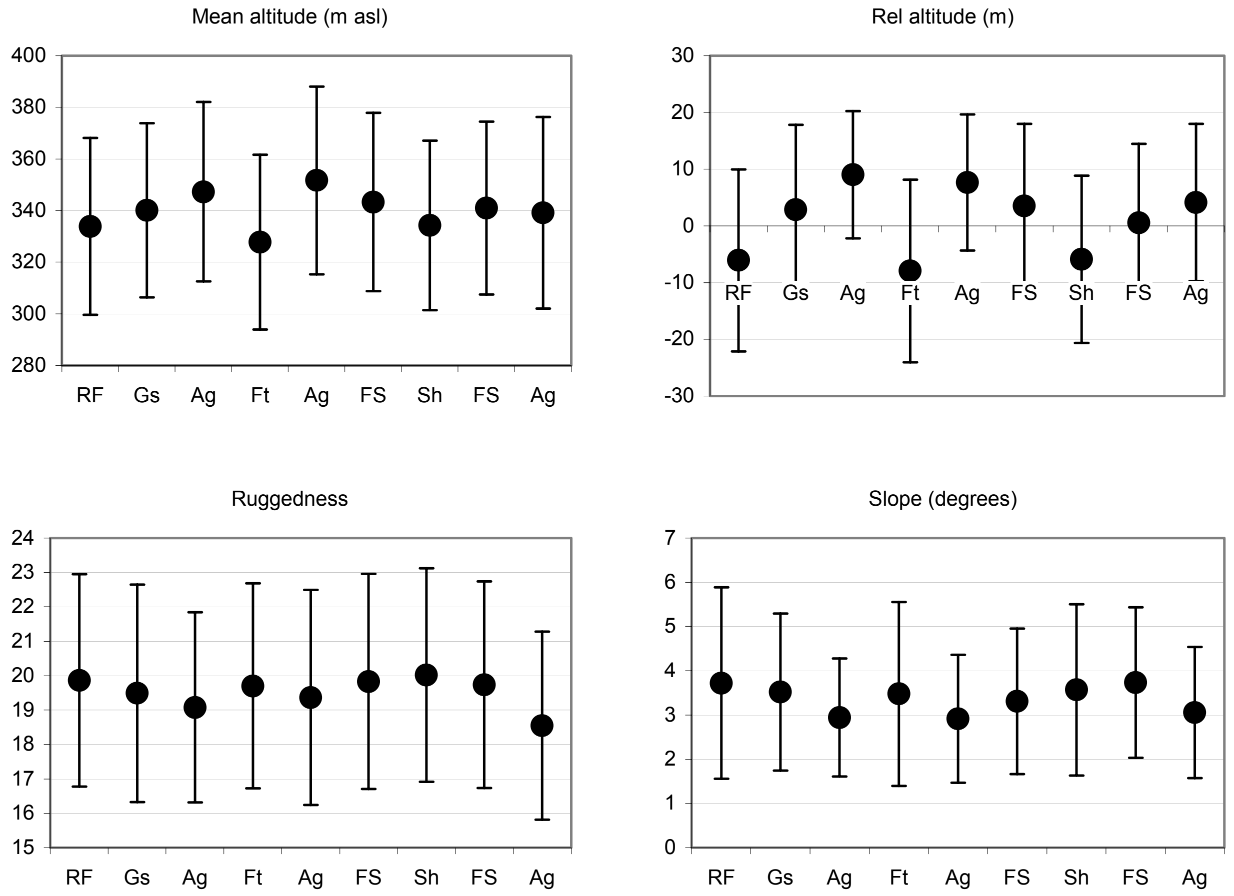


Figure 5. Terrain characteristics of the land-units in Vacaria: mean ± SD. Legends of the land-units in the X axis as in Figure 6.

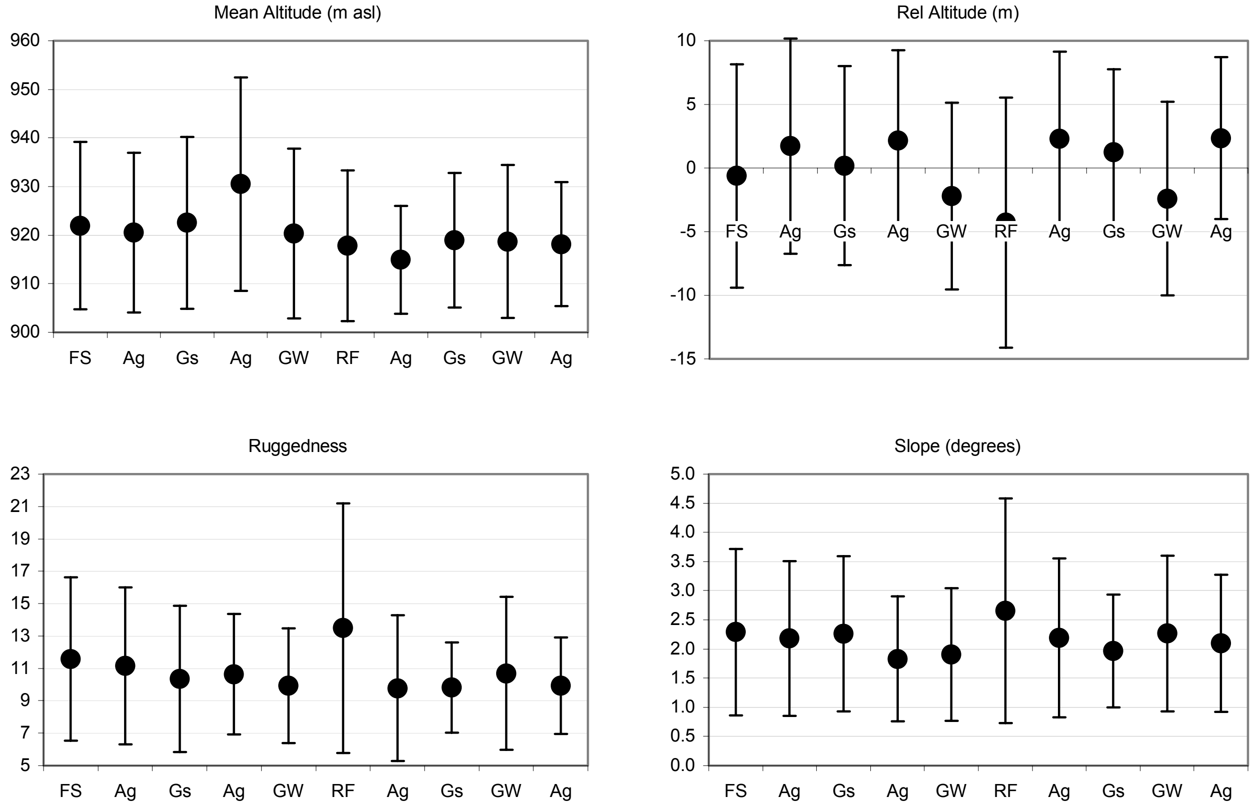


Figure 6. Terrain characteristics of the land-units in Cambará: mean ± SD. Legends of the land-units in the X axis as in Figure 6.

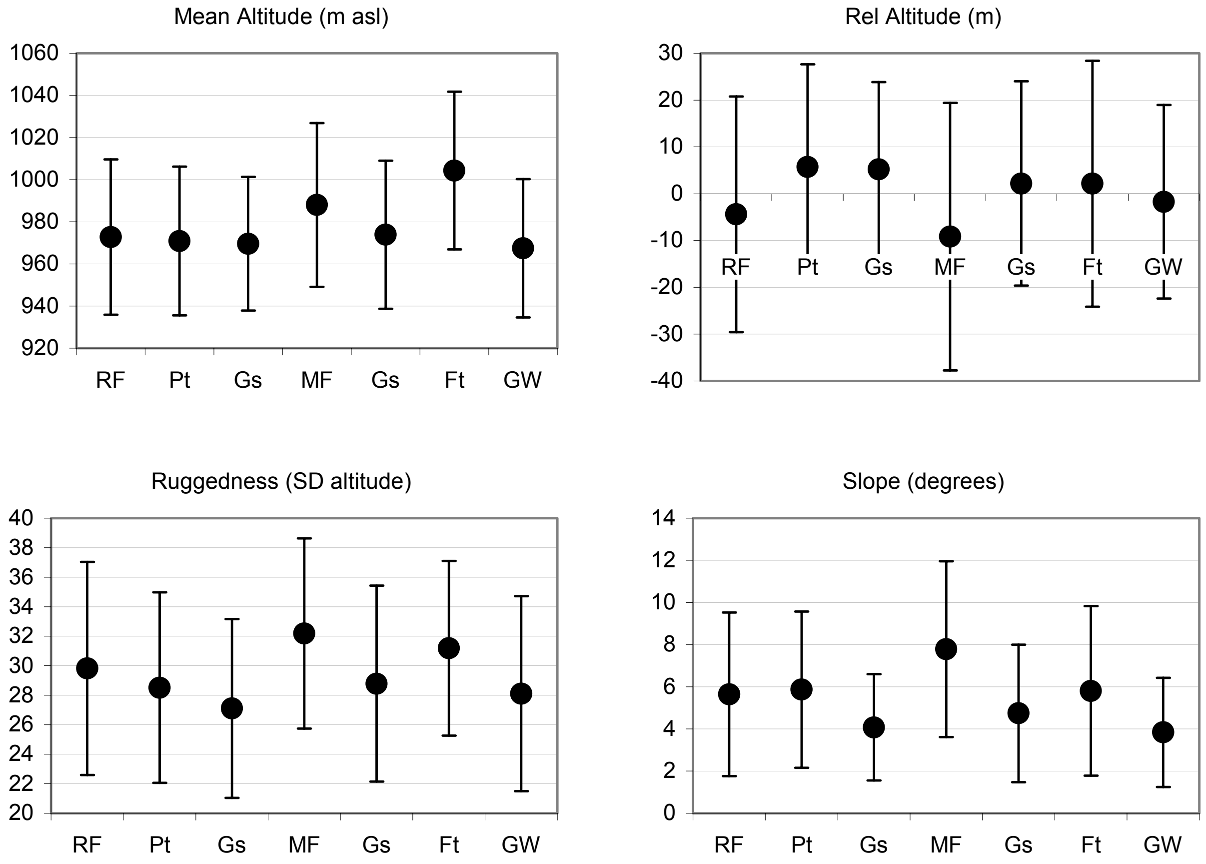
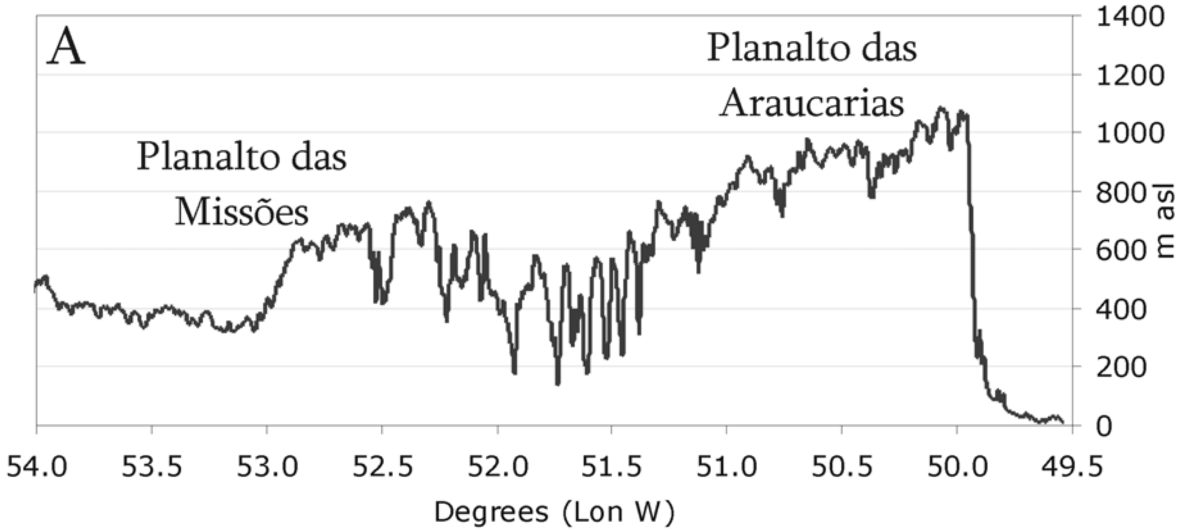


Figure 7. Topographic profiles in the study area. Transect A follows the 29°S parallel. Transect B follows the 50.6°W meridian. Digital Terrain Model from Miranda (2005).



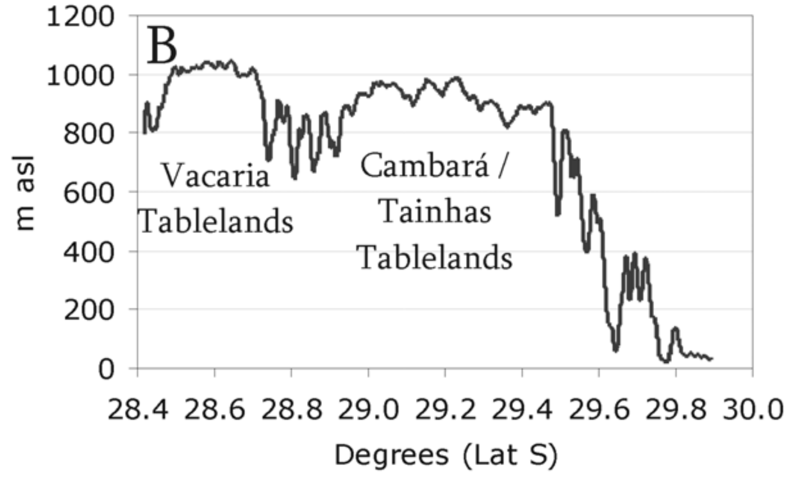


Figure 8. Seasonal mean rainfall (± SD) from 1949 to 1998. JFM: Austral summer; JAS: Austral winter. Sites, coordinates and altitude within the graphic box. Data source: Instituto Nacional de Meteorologia (INMET), 8o Distrito, Porto Alegre, Brazil.

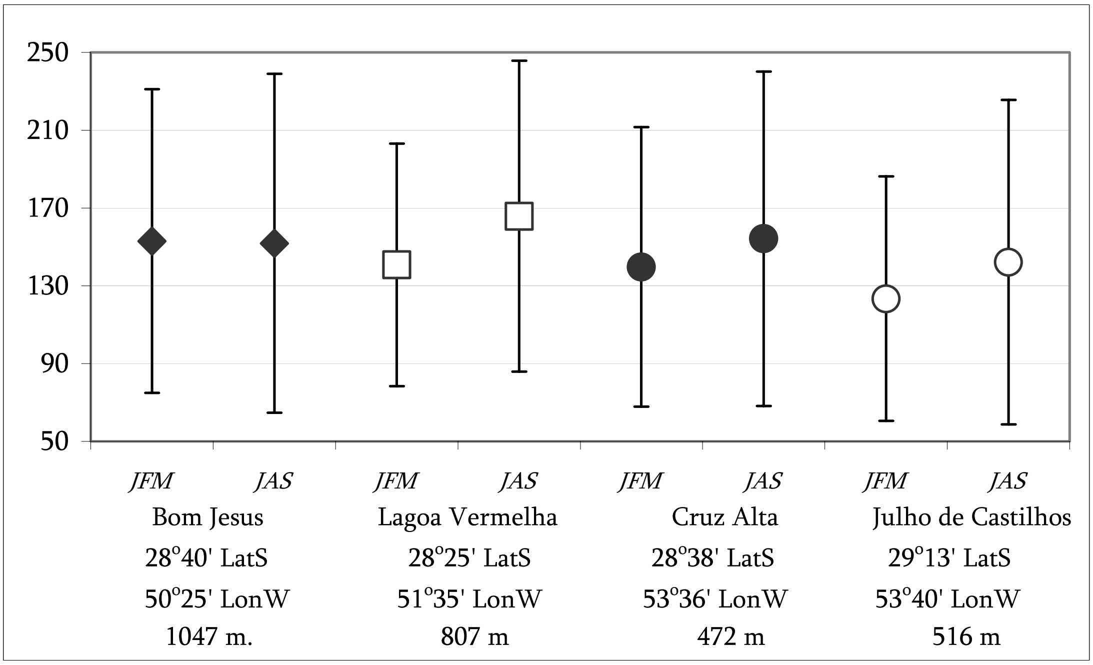
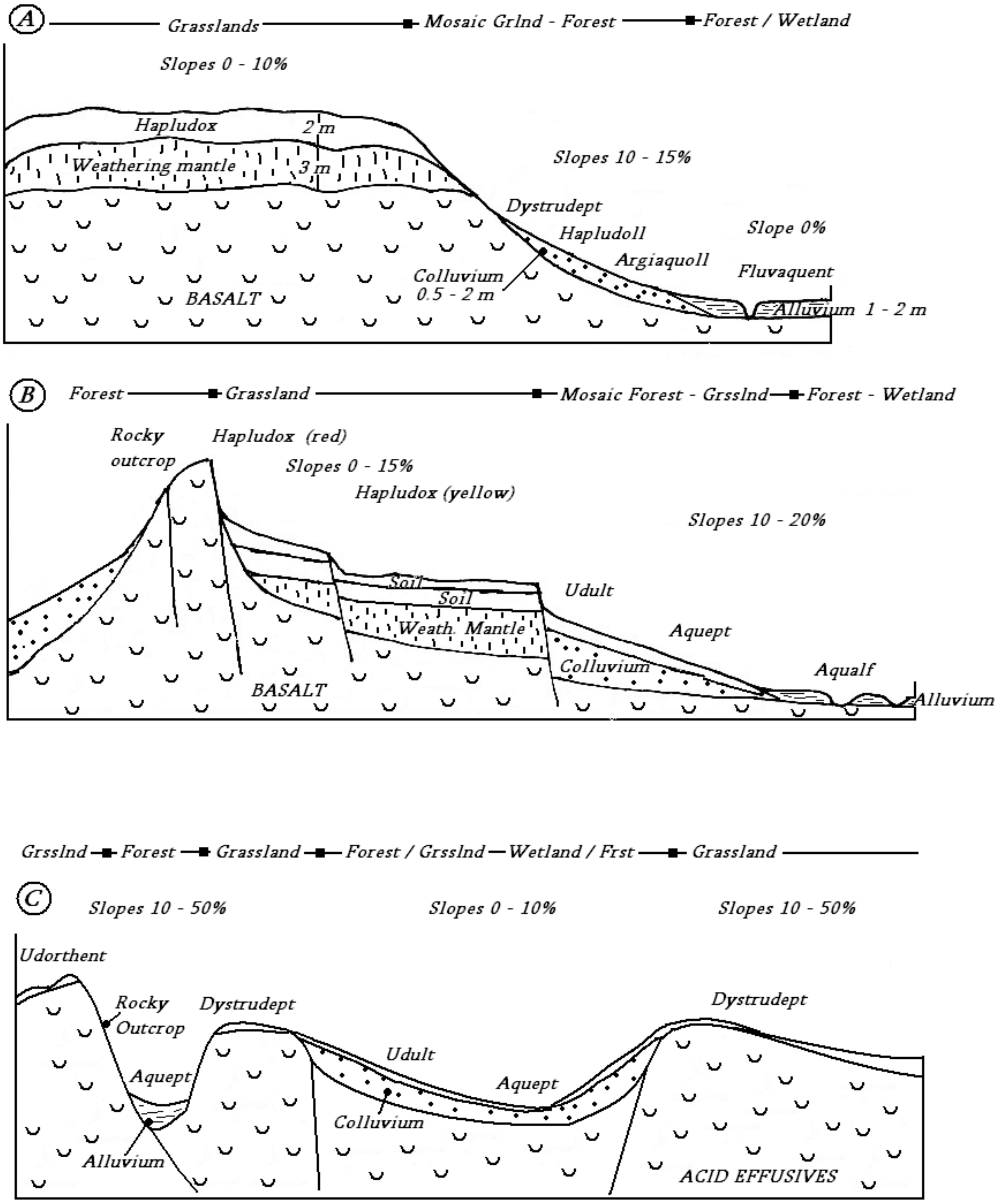
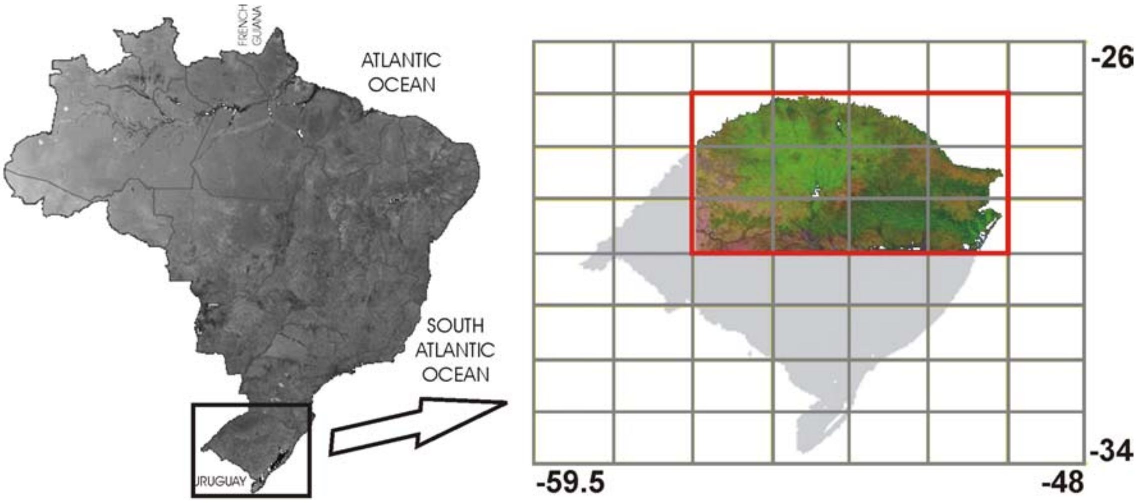


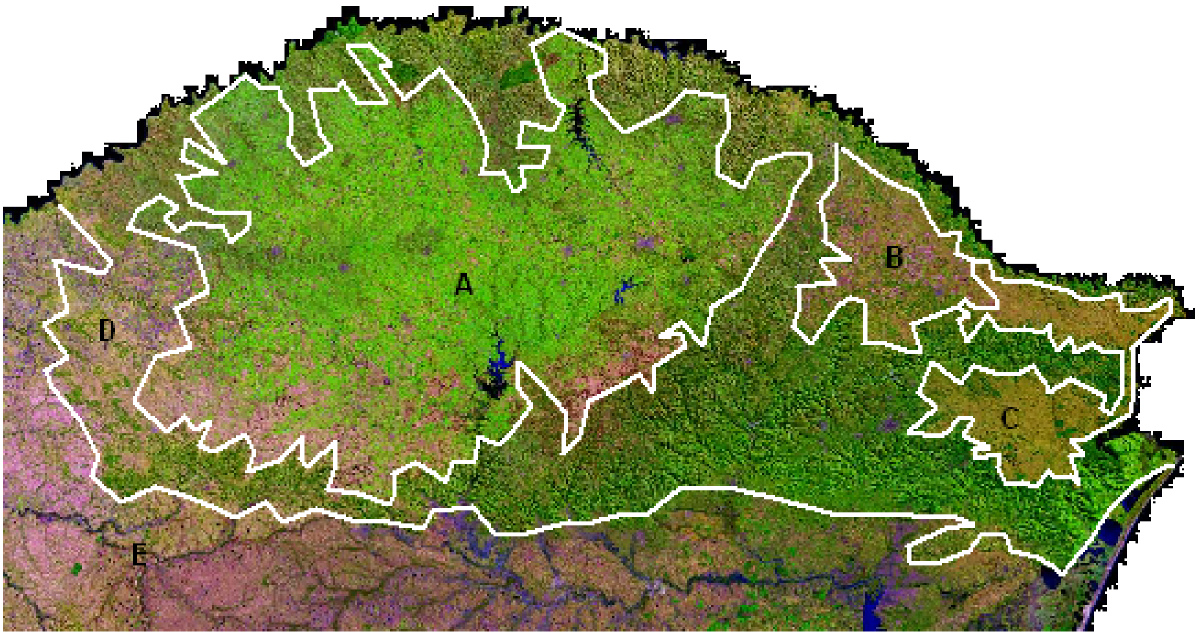
Figure 9. Idealized vegetation – soil - landform profile in the three landscape types of the tablelands. A- *Planalto das Missões* type, B – *Vacaria* tablelands type, C – *Cambará/Tainhas* tablelands type.



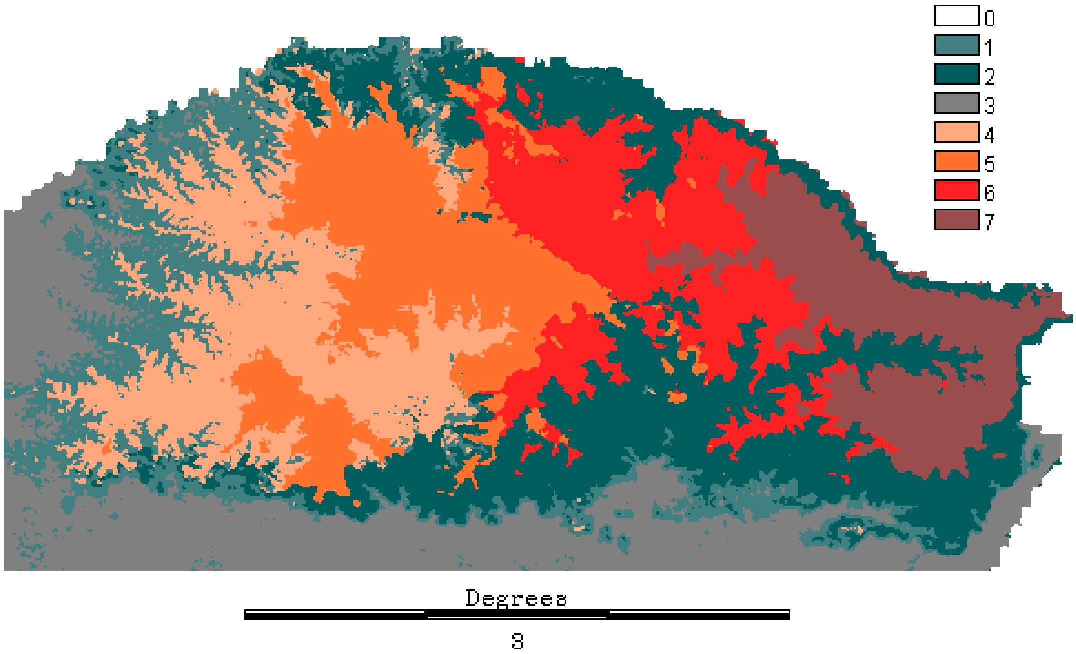
Map 1. The location of the study area. Grid in right panel gives geographical coordinates. Study area enclosed by red box.



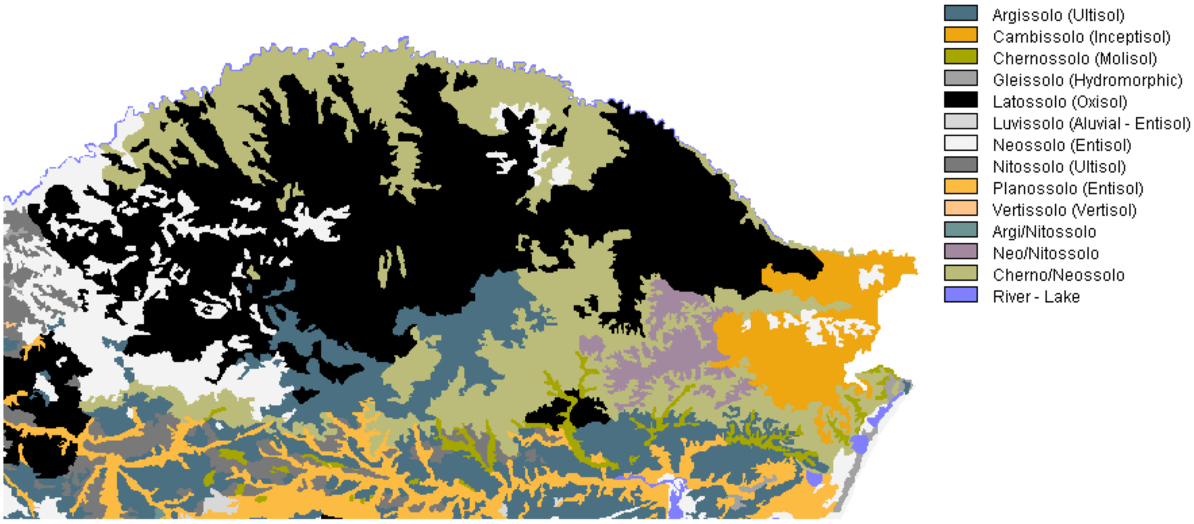
Map 2. The study area, subdivided into first-order landscape types according to a preliminary classification based on literature, field survey and visual interpretation of false-color composites. Unit A: *Planalto das Missões*. Units B + C: *Planalto das Araucárias* (unit B: *Vacaria* tablelands; unit C: *Cambará/Tainhas* tablelands). Unit D: Sierra. Unit E: lowlands.



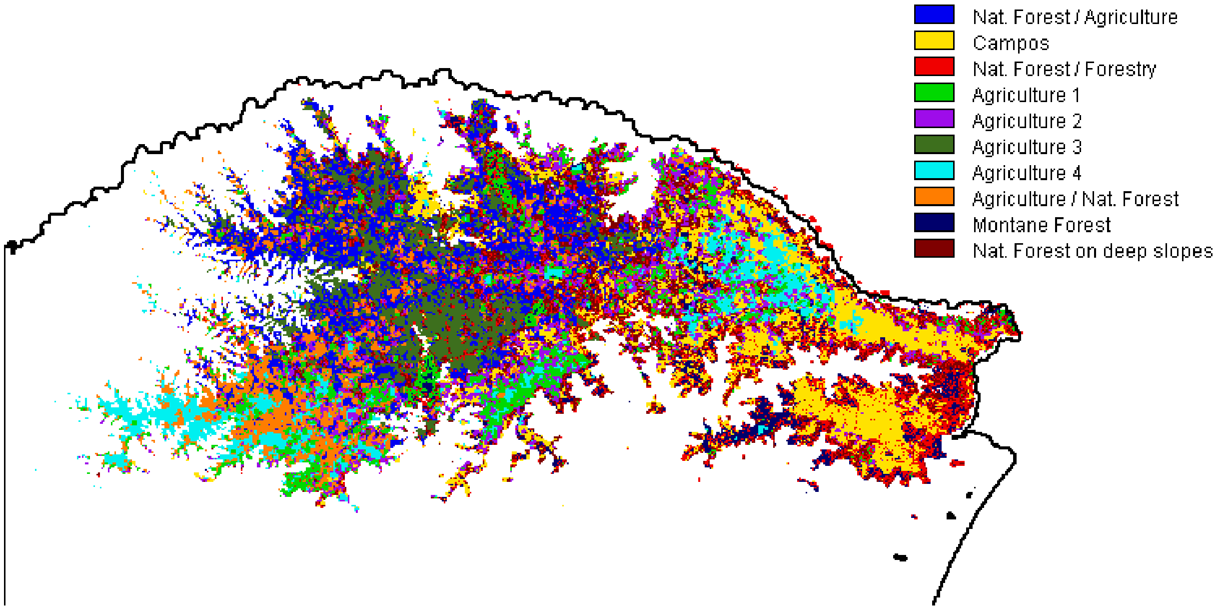
Map 3. First order landscapes according to a classification based on topographic traits. 0: background, 1 + 2: Sierra domain, 3: lowlands, 4 + 5: *Planalto das Missões* domain, 6: transitional between the *Planalto das Missões* and the Sierra, 7: *Planalto das Araucárias*.



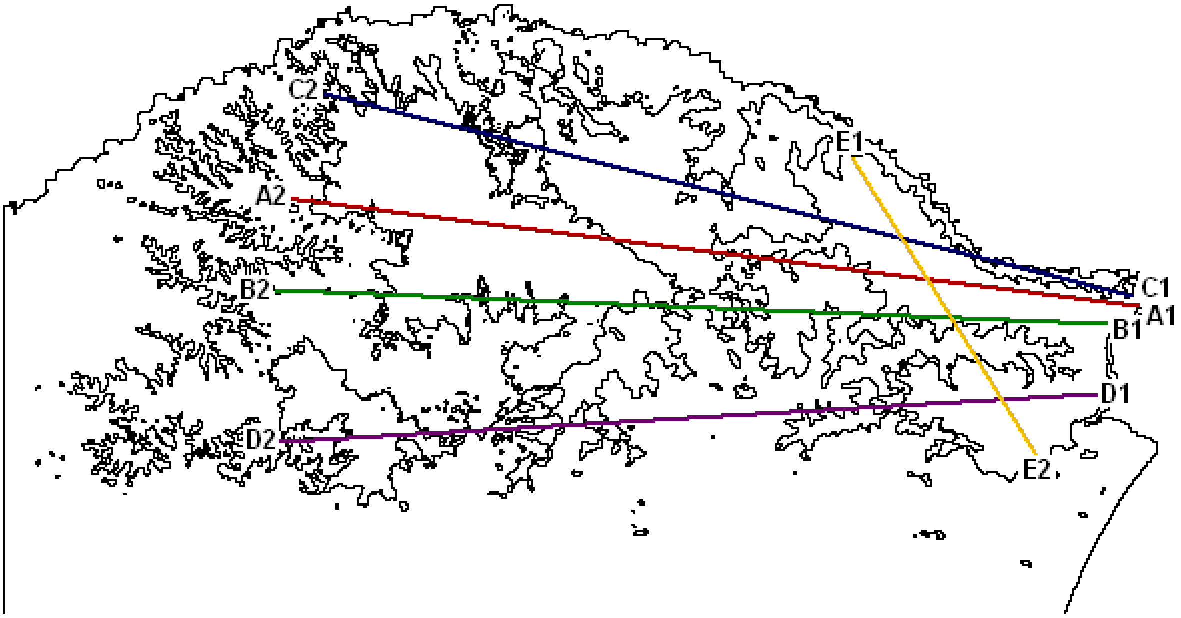
Map 4. Section of the general map of soils in the study area, according to BRASIL 1973. Classes were updated to the currently accepted Brazilian Soil Classification System (BSCS: EMBRAPA, 1999) by Streck *et al.* (2002). Correspondence between the BSCS and the USDA Soil Taxonomy (classes in brackets) according to EMBRAPA (http://www.cnps.embrapa.br/sibcs/index.html).



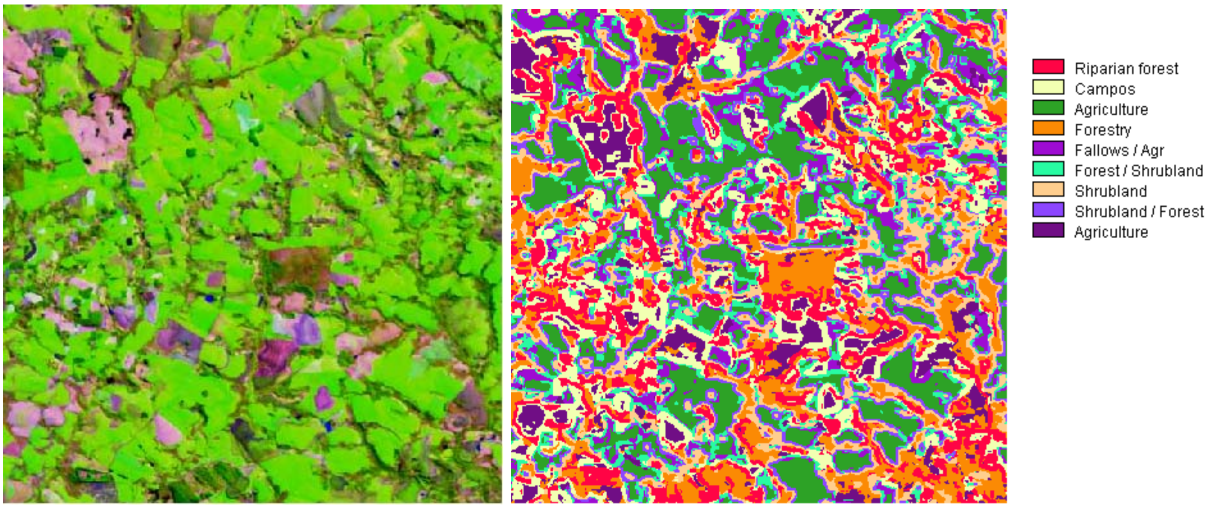
Map 5. Second order landscapes within the tablelands, according to a classification based on Landsat imagery (bands 5, 4 and 3).



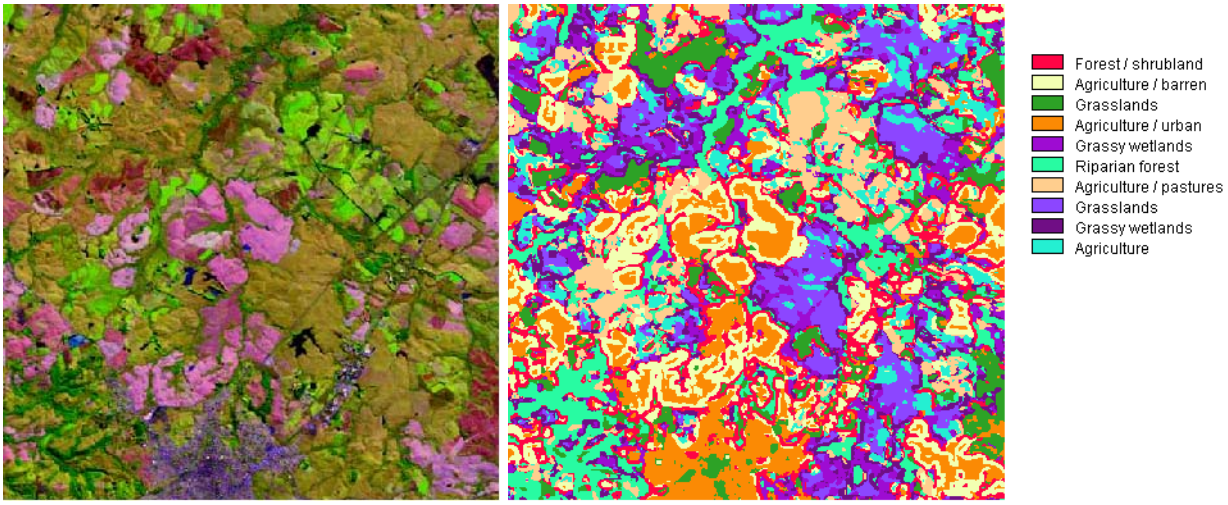
Map 6. Five regional transects for surveying the spatial association of soils and land-units within the topographic domain.



Map 7. (a) False color RGB-composite of a window in the *Planalto das Missões*, Landsat bands 5, 4 and 3 for the red, green and blue channels, winter 2001. (b) Corresponding land-unit classification based on the same imagery. Image central point at: 28°11’15”S / 54°11’15”W, 500 x 500 pixels, proximate pixel size 30 m.



Map 8. (a) False color RGB-composite of a window in the *Vacaria* tablelands, Landsat bands 5, 4 and 3 for the red, green and blue channels, winter 2001. (b) Corresponding land-unit classification based on the same imagery. Image central point at: 28°26’15”S / 50°56’15”W, 500 x 500 pixels, proximate pixel size 30 m.



Map 9. (a) False color RGB-composite of a window in the *Cambará/Tainhas* tablelands, Landsat bands 5, 4 and 3 for the red, green and blue channels, winter 2001. (b) Corresponding land-unit classification based on the same imagery. Image central point at: 29°03’45’’S / 50°11’15’’W, 500 x 500 pixels, proximate pixel size 30 m.

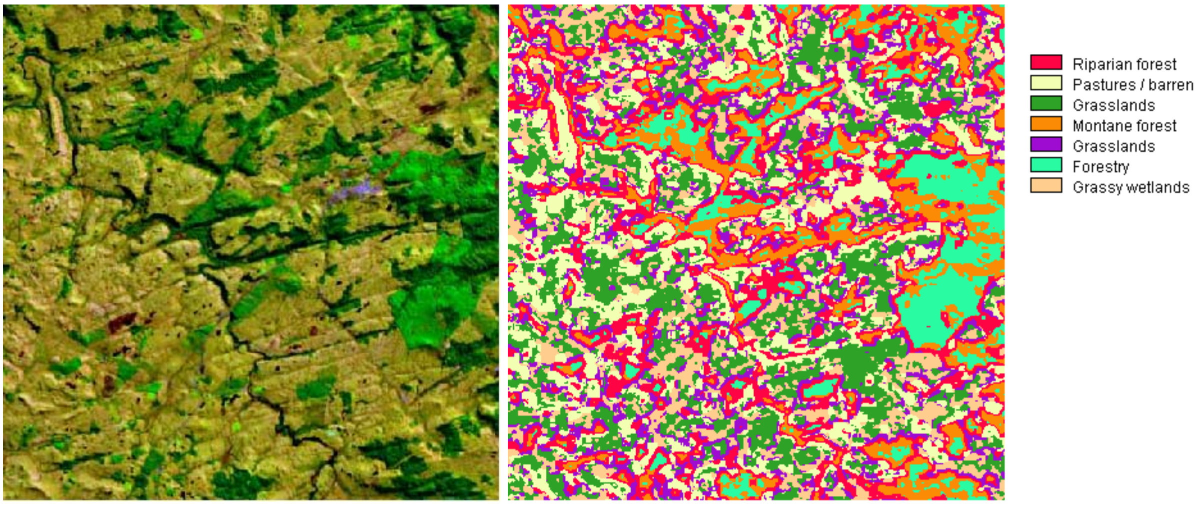


Photo 1. Grassland and montane forest in a temporally waterlogged depression, in the Cambará/Tainhas tablelands (29º03’99’’S, 50º57’21’’W, 814 m asl). Notice the tussocky grassland to the front, occupying the lower position in the topographic catena. On a slightly higher position, a fringe of montane forest extends between the bottomlands and campos covering the surrounding hills.

Photo 2. Montane forest dominating on top of a topographic catena in the Cambará/Tainhas tablelands. (29º03’99’’S, 50º57’21’’W, 850 m asl).

SECTION 2

ECOSYSTEM FUNCTIONAL TYPES FROM MODIS LAI / FPAR AND MODIS VEGETATION INDICES: OPERATIONALITY AND TECHNIQUES

CHAPTER 3. ECOSYSTEM FUNCTIONAL TYPES FROM MOD13 AND MOD15 IMAGERY: A FUNCTIONAL CLASSIFICATION FOR SOUTHERN BRAZIL

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RESUMO

Tipos funcionais de ecossistemas (TFEs) referem-se a entidades espaciais que são definidas na base de trajetórias sazonais similares de algum processo relacionado com a troca de matéria e energia da vegetação. Essas entidades descrevem a heterogeneidade funcional numa região. Neste trabajo nós desenvolvemos um método para classificar TFEs a partir de dinâmicas sazonais similares de parâmetros Modis: LAI/FPAR e NDVI, ao longo de um ciclo anual. Mudanças funcionais de mais longo praço devem ser descritas mediante a comparação de classificações correspondentes a vários anos. Como um simples ciclo anual é considerado cada vez, a classificação funcional pode resultar sensível em excesso ás variações aleatórias de clima o de fatores biológicos.

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Assim sendo, é necessário avaliar quanto os TFEs realmente descrevem padrões ecologicamente significativos de variabilidade funcional. Os TFEs devem, por tanto, se ajustar a alguns enunciados: 1- o funcionamento dos ecossistemas é um atributo multidimensional da vegetação em relação ao seu ambiente. 2- esse funcionamento pode ser descrito de multiplas maneiras, as quais serão interligadas. 3- Porém, cualquer uma que for a definição de funcionamento a partir da qual a heterogeneidade é descrita, deve se manter que a classificação de TFEs responde sensivelmente aos padrões de distribuição da fisionomia da vegetação, do uso da terra e de outros controles ambientais.

Quanto ao primeiro e segundo enunciados, nós achamos que os TFEs produzidos a partir de bases de dados Modis Lai/Fpar e Modis NDVI divergiram em termos da sua riqueza e arranjo espacial das classes. Porém, a interação entre classificações, medida pelo Coeficiênte de Coherência, foi altamente significativo e numericamente robusto. Quanto aos enunciados primeiro e terceiro, nossos resultados mostram uma interação extremamente significativa entre as classificações funcionais e controis ambientais e vegetacionais. Os padrões de distribuição desses controis foram representados por mapas de cobertura da terra e unidades regionais de solos. A interação entre eles, no entanto, foi medida por um análise tridimensional de informação. O 70 porcento da informação associada á classificação baseada nos parâmetros Lai/Fpar devio-se á interação dos TFEs com unidades de cobertura da terra e solos. No entanto, o 77 porcento da informação associada com a classificação baseada no NDVI a uma interação similar. Todavia as classificações funcionais apresentam uma porção da sua informação não explicada pela interação e deve ser atribuida a outros fatores (i.e. dinâmica sucessional, freqüência e intensidade de distúrbios como o fogo e epidemias). Em termos gerais, a forma da interação entre os tipos funcionais de ecossistemas e a estrutura da vegetação é altamente dependente do contexto ambiental. Por tanto, tipos de vegetação estruturalmente diferenciados e que ocorrem em condições ambientais diversas, podem converger numa única classe funcional.

Visto que os TFEs obedecem nossos enunciados teóricos, nós temos desenvolvido conceitual e metodologicamente os tipos funcionais de ecossistemas, para apoiar a pesquisa de processos extremamente dinâmicos de alteração funcional em resposta a mudanças igualmente rápidas da dinâmica do clima e de uso da terra.

Palavras chave: Heterogeneidade funcional, tipos funcionais de ecossistemas, trajetórias sazonais, Lai, Fpar, Ndvi, interação de classificações, análise de informação em três dimensões.

ABSTRACT

The term ecosystem functional types (EFTs) was coined to specify collections of spatial entities defined on the sole basis of similar seasonal dynamics of some process related to the matter and energy exchange of the vegetation. These entities serve to describe the functional heterogeneity of a given region. In this paper we develop a method to classify pixels into groups that satisfy our definition of EFTs. We do this on the basis of a common seasonal dynamics of the MODIS LAI/FPAR and MODIS NDVI, along a single annual cycle. Trends of longer-term changes should then be inferred from the comparison among several years. As just one annual cycle is considered each time, the functional classification may turn out to be too sensitive to random variations of the climatic and/or biological factors influencing functional heterogeneity in the vegetation space. It was therefore necessary to assess to what extent the resulting pixel groups satisfy some essential EFT criteria: 1- ecosystem functioning is a multidimensional attribute of the vegetation in relation to its environment, 2- as such, ecosystem functioning may be depicted in several distinct, yet interrelated ways, 3- but whatever the chosen definition of ecosystem functioning, it should hold true for the derived classification and respond sensitively to distributional patterns of vegetation physiognomy, land-use and environmental drivers.

Regarding the first and second tenets, we found that the EFT maps produced from the MODIS LAI/FPAR and the MODIS NDVI datasets diverged in terms of the richness and spatial array of their classes. However, the interaction between maps, as measured by means of an information theoretical Coherence Coefficient, was highly significant and numerically robust. Regarding the first and third tenets, our results show that both EFT maps had a strong and highly significant interaction with vegetational and environmental controls. These controls were represented by a map of land-cover and soil units. Interaction was assessed by means of information analysis in three-dimensional contingency tables. We found as much as 70 percent of the information associated with the LAI/FPAR classification due to its interaction with soils and land-cover types, while 77 percent of the information associated with the NDVI classification explained by the same set of vegetational and environmental factors. These facts notwithstanding, the functional classifications also present some information that remains unexplained and should be attributed to other factors (such as successional dynamics, fire frequency and intensity of disease outbreaks). In general terms, the shape of the interaction between ecosystem functioning and vegetation structure is highly dependent on the environmental context. As such, structurally-different types of vegetation occurring under different environments, may converge into a unique functional class.

Given that the EFTs comply our theoretical tenets, we have further developed the EFTs, both conceptually and methodologically, to withstand the rapid paces at which spatial patterns of functional heterogeneity may change in response to highly dynamic land-use and climate drivers.

Key words: Functional heterogeneity, ecosystems functional types, seasonal trajectories, LAI, FPAR, NDVI, classifications interaction, thee-dimensional information analysis.

Running title: Ecosystem functional diversity in Southern Brazil.

INTRODUCTION

Ecosystems and ecosystem functional types

Functioning is at the very core of the ecosystem concept. Ever since the pioneering works of R. Lindeman (1942) and E.P. Odum (1969), ecosystem ecology has placed major emphasis onto the processes active in the inter-phase of the ecosystem's physical, chemical and biological components (Shugart 1988). Central to this science are the tasks of detecting and interpreting spatial patterns of functional heterogeneity, which in turn reflect the spatial variation of the environmental template (Turner & Chapin, 2005) and the composition of plant functional types in a given region (see Orlóci & Orlóci 1985, Pillar & Orlóci 1993, Diaz & Cabido 2001, and references therein).

Functional heterogeneity is of fundamental importance to forecast ecosystem responses to global change, a subject with societal consequences that extend well beyond the scope of Ecology itself (De Leo & Levin, 1997). However, it has been recognized that to lay open the functional properties of the ecosystem is a much more difficult task than to describe its structural features. Whenever it comes to mapping the actual geographical distribution of ecological units as ecosystems, the functional criterion is frequently subordinated to that of vegetation structure, in a way that functional traits are drawn from a few study plots and then extrapolated to the total coverage of structurally delimited units. The approach, which assumes a direct and spatially homogeneous connection between function and structure, made possible to broaden ecological knowledge over rather complex ecosystems and processes, as can be seen in Odum (1960), Lieth (1975), Sarmiento (1984), Sala & Austin (2000) and Sarmiento *et al.* (2004), to cite a few examples. Interestingly, the spatio-temporal uncertainties of the connection between function and structure have been left largely untested.

Milchunas & Lauenroth (1995) and Pennington (1986) noticed that, to given scenarios of environmental change, the paces of response of ecosystem function and structure may differ significantly. In turn, if on the one hand there exists a variable degree of functional diversity within structurally defined vegetation units, on the other, it is also possible that structurally divergent types of vegetation share similar functional patterns. This scenario stresses the need for independent recognition and characterization of functional entities, in a way that the relation between function and structure, at the ecosystem level, can be empirically analyzed and inferred instead of assumed '*a priori*'.

The term "ecosystem functional types" (in short, EFTs) was coined by Paruelo *et al.* (2001) to specify spatial entities defined on the sole basis of similar seasonal traits of the Normalized Difference Vegetation Index (NDVI). Thereafter, EFTs were applied to describe the functional heterogeneity of temperate South America (Paruelo et al. 2001) and the Iberian peninsula (Alcaraz et al. 2006). In both cases, the authors used the ca. 20 years long, global AVHRR-NDVI database to calculate multi-year, average statistics of the spectral response of the vegetation. These were then used to pool pixels together into functionally homogeneous groups.

Although the researchers found a strong correspondence between the ecosystem functional types and observable features of the vegetation (such as land-use and phytogeographic patterns), implicitly assumed was that the analyzed regions remained functionally stable over time covered by the AVHRR database, with interannual changes relegated to mere random variation around an average behavior. However, drastic changes of the environmental setting, with considerable effects on the vegetation, may occur as fast as to make this assumption untenable. During the Late Quaternary some severe climate transitions took place at time scales of less than a decade (Adams *et al.,* 1999). Moreover, global economic forces manage to profoundly alter regional patterns of land-use and plant-cover within a dozen of years. As we have witnessed in our study area, the spatial distributions of plant cover may drift so fast, that the spatial share of ecosystems is very likely to change from one year to the next. In order to reflect on the influence of highly dynamic climate and economic drivers, whose action upon ecosystem functioning can be better captured by analyzing patterns of change at a detailed temporal scale, we aim at a method to define ecosystem functional types that is sensitive to the year-to-year spatial variability of functional entities.

Therefore, we start with the concept of EFTs as stated by Paruelo *et al.* (2001), in which the functional units enclose areas with a common seasonal dynamics of variables related to the carbon and energy exchange of the vegetation. However, we trace this dynamics season by season, along a single annual cycle, which is to say that we are independently assessing spatial patterns of functional heterogeneity for each year. Trends of longer-term changes should then be inferred from the comparison of several years. As just one annual cycle is considered each time, the functional classification may become too sensitive to random variation of the climatic and/or biological factors influencing the spatial pattern. If so, the mapped heterogeneity and its multiyear variation would lack interpretability in terms of meaningful trends of ecosystem response to environmental or land-use change. It is therefore absolutely necessary to examine to what extent year-specific ecosystem functional types actually comply with some essential tenets: 1- ecosystem functioning is a multidimensional attribute of the vegetation in relation to its environment, 2- as such, ecosystem functioning may be depicted in several distinct, yet interrelated ways, 3- but whatever the chosen definition of ecosystem functioning, it should hold true for the derived classification that it responds to distributional patterns of vegetation physiognomy, land-use and environmental drivers.

To test the interconnected nature of classifications resulting from different definitions of ecosystem functioning, we identified EFTs on the basis of two different proxies of the vegetation functional activity: MODIS NDVI and the interplay of MODIS LAI / FPAR. We measure to what extent their results express both commonalities and differences. To test the sensitiveness of the EFTs to the vegetational and environmental determinants, we transform the classifications into thematic maps which we contrast to maps of soils and land cover types, seeking commonalities and differences. For the case, we rely on soils to represent the spatial distribution of crucial environmental variables, since soils are stable and dependable indicators of climatic, geomorphic and biological processes of key importance for ecosystem functioning. Likewise, we rely on a land-cover classification based on dominant physiognomy and land-use to represent the spatial variation of important vegetational drivers. We assume that for the preliminary goals of this work and at the regional scale of our analysis, these two parameters hold sufficient information with regard to those adaptive traits of the vegetation that are influential on the distinctive traits of the matter and energy exchange of local ecosystems.

Primary data: The MOD13 and MOD15 imagery

Satellite-recorded spectral reflectances of the plant cover have been shown to be reliable proxies of ecosystem functioning (Running *et al.* 2000). The Normalized Difference Vegetation Index (NDVI), for instance, allows straightforward estimation of the fraction of photosynthetically-active absorbed radiation (FPAR), while both, the NDVI and the Enhanced Vegetation Index (EVI) are related to the carbon-gain dynamics of the primary producers (see Ferreira & Huete 2004, and references therein). This fact has supported the development of models with partial or total reliance upon remotely sensed data, such as the GLOpem model of Prince & Goward (1995), and the classification of vast areas of the world's vegetation on the base of selected traits of the vegetation spectral responses (Tucker *et al.* 1985, 1991, Stone *et al.* 1994, DeFries *et al.* 1998, and references therein).

The advent of the Moderate Resolution Spectro-radiometer (MODIS), operating on-board the Terra and Aqua spacecrafts and acquiring data in 36 spectral bands between 0.405 and 14.385 µm (Justice *et al.* 1998), is highly significant in this context. The derived products include Spectral Vegetation Indices (Normalized Difference VI: NDVI and Enhanced VI: EVI), Net Photosynthesis and Gross Primary Productivity (NPS and GPP), Leaf Area Index and Fraction of Photosynthetically-active Absorbed Radiation (LAI and FPAR; Parkinson & Greenstone 2000), with temporal resolutions varying from 8 days to one year, and with spatial resolutions ranging from 0.06 to 1 km^2. Given these characteristics, MODIS time-series represent a significant gain in terms of multidimensionality and detail drawing, when it comes to assess ecosystem functioning and its spatial variability.

MODIS spectral vegetation indices (VIs: MOD13 datasets) contain two functional variables: the normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI), which have been used to set differences among the various physiognomic types within the *Cerrado* and the tropical forest biomes (Huete *et al.* 2002, Ferreira & Huete 2004 and Ratana *et al.* 2005), to assess the impact of forest fragmentation in the legal Brazilian Amazon (Ferreira *et al.* 2007), and, also in that region, to disclose different responses to the dry season by natural forests and secondary grasslands (Huete *et al.* 2006). These datasets have a temporal resolution of 16 days and three different pixel sizes: 1, 0.25 and 0.0625 Km^2.

The two functional variables in the MOD15 collection are, in turn, the leaf area index (LAI) and the fraction of photosynthetically active radiation absorbed by the vegetation cover (FPAR). Asner *et al.* (2003) and Berclay (1998) stressed the value of the leaf area index as an ecological indicator of vegetation activity, since the amount of foliage contained in plant canopies emerges from the phenological response of the vegetation under the integrated influence of nutrient dynamics, herbivores activity and climatic conditions. For the MOD15 dataset, LAI was defined as one-sided green leaf area per unit ground area in broadleaf canopies, and as the projected needle leaf area in coniferous canopies (Myneni *et al.* 1997; Knyazikhin *et al.* 1999; Myneni *et al.* 2002). Likewise, FPAR mirrors the temporal dynamics of carbon assimilation (Running *et al.* 2000), manifesting how the constraints imposed by environmental forcings interact with the adaptive traits of the primary producers. The MOD15 collection has a temporal resolution of 8 days and a spatial resolution of 1 km^2.

Both LAI and FPAR can be estimated from spectral vegetation indices (VIs) with variable degree of accuracy (Myneni *et al.* 1997, Broge & Leblanc 2000). However, while the relation between the VIs and FPAR is closely linear, the VIs cease to be sensitive proxies of the green biomass accumulation when LAI exceeds an average magnitude of three (Broge & Leblanc 2000). The MOD15 algorithm (Khyazikhin *et al.* 1997, Myneni *et al.* 2003) was designed on the basis of a radiative transfer model (Myneni *et al.* 1997) to make direct use of the hyperspectral records of the MODIS sensor, allowing a more precise calculation of both parameters without LAI saturation problems. These antecedents speak for the potential of using MOD13 and MOD15 imagery to examine the linkage between ecosystem function, vegetation structure and environmental controls.

THE ENVIRONMENTAL SCENARIO OF FUNCTIONAL HETEROGENEITY

Ecosystem functional types were identified, for the annual cycle of 2002, within the portion of the State of Rio Grande do Sul in Brazil bounded by 28° to 30°S, and 51° to 49°30'W (Figure 1A). From the climate viewpoint, the study area belongs to the ecotone between humid subtropical and humid temperate formations of southern South America, with mild winters, warm summers and annual rainfalls above 2000 mm (Nimer 1990). Yet, it should be noticed that the annual cycle of 2002, chosen for characterizing functional heterogeneity, was remarkably atypical both in terms of rainfall and temperature (Figure 2), starting with a colder and drier-than-normal summer, followed by a colder yet rainier winter and a spring season with rainfall totals well above the historical mean. According to the US National Oceanic and Atmospheric Administration (www.noaa.gov), a moderate El Niño episode started to develop in February that year and attained full strength 4 to 8 months later, which provides a plausible explanation for the abnormal behavior of the regional climate during the period.

In the study area, topography is the principal determinant on both local climate and vegetation composition. The broad regional topography is the product of the passive-margin Late-Tertiary and Quaternary tectonics (see Pinillos *et al.*, Chapter 2 this thesis, and references therein) which lifted and broke the continuity of a massive Cretaceous-effusive mantle of the *Paraná* Geologic Province. Consequence of this tectonics in northern Rio Grande do Sul is the basaltic plateau, subdivided by faulting and river erosion and dissection into the *Planalto das Araucarias* and the *Planalto das Missões*. The plateau upheaval determined the relative sinking of the neighboring Paleozoic - Mesozoic sedimentary basin (Central Depression), and intensified the erosion–deposition processes along the faulting system towards the Central Depression and the Coastal Plain (FIBGE 1986, Schobbenhaus *et al.* 1984). Major products of this tectonic and geomorphic dynamics are recognizable by the division of the area into four major types of landscapes (Figure 1B)¸ each one with their distinctive natural vegetation and environmental setting: 1- The Quaternary coastal plain, 2- the central depression, 3- the *Serra Geral* and 4- the tablelands lying atop the plateau.

The Quaternary coastal plain is a complex of lacustrine, riverine and shore deposits that were naturally dominated by tropical rain-forests, *restingas*, (sclerophyllous scrublands and low forests on quartzitic substrata), and swamps. Under the influence of the warm Brazilian Current, the unit exhibits an ever-wet, warm regime with moderate differences between the coldest and the warmest months. Given its characteristic low thermal amplitude, the area is the southernmost extension of Brazilian tropical coastal ecosystems. The Central Depression is the easternmost extension of an ancient pediplain that developed on a Paleozoic – Mesozoic sedimentary basin. It was formerly occupied by grasslands on the remnant surfaces of the pediplain, and by semi-deciduous forests on highly dissected terrains and outcrops of the Jurassic sandstone.

The '*Serra Geral*' or High-Plateau escarpment comprises the sierra relief, bordering the plateau. Dominated by shallow, young soils, different types of forest are the natural cover of the area: semideciduous in the western to southern slopes, tropical per-humid on the seaward slopes and mixed *Araucaria*-broadleaf forests in the upper altitudinal belt. The basaltic high tablelands (High Plateau) are also the result of a long pediplanation process, though the influence of tectonics is evident. Subtropical grasslands covered most of the relict surfaces in the area, while *Araucaria*-dominated forests occupied the galleries and the soil-stripped hills along the faulting system. In summary, natural vegetation includes different types of grasslands, locally known as *Campos*, semi-deciduous forests, evergreen, mixed *Araucaria*-broadleaf forests and evergreen, broadleaf Atlantic rainforests (FIBGE 1986, Pillar & Quadros 1997). Additional information on the natural vegetation patterns of the area can be found in FIBGE (1986), Pillar & Quadros (1997), Pillar (2003), Oliveira & Pillar (2004) and Pinillos *et al.* (2007, Chapter 2, this thesis).

Likewise, land-use types occur across the area following a rather predictable pattern. In the spatial domain of the plateau, extensive cattle-raising dominated the grasslands for the last three centuries until recent process of land-use intensification took over: cash crops on the deep, lateritic soils, commercial afforestation on the shallow soils with little agricultural value, and animal husbandry intensification (by the genetic improvement of the herd and the introduction of exotic forages: Bristol 2003) on most of what remained of the original *campos*.

In the *Sierra Geral*, along the valleys formerly dominated by forests, small-farm horticulture occupies the rich and well drained soils. On the hills, extensive pine and *Eucalyptus* plantations encroach mainly upon semideciduous and mixed *Araucaria*-broadleaf forests. Banana plantations extend onto the lower altitudinal belt of the Atlantic slope, at the expense of the tropical per-humid communities. The Coastal Quaternary riverine and lacustrine terrain has been used for cattle raising, now extensively transformed into agriculture (rice) and forest plantations, while shoreline landforms increasingly support urban development. In the portion of Central Depression within the study area, the most dissected surfaces increasingly support *Eucalyptus* spp. and *Acacia* spp. plantations, while the older soils on the pediplain relict surfaces are widely used for small-farming agriculture, cattle raising and commercial afforestation.

METHODS

Identification of the Ecosystem Functional Types

The problem of identifying EFTs is approached sequentially. In agreement with the original concept (Paruelo *et al.* 2001), functional seasonality is the key criterion to differentiate functional classes. Our method traces, throughout a given annual cycle (e.g. 2002), the seasonal functional trajectory of each pixel, identifies significant patterns among the trajectories and then pools the pixels together according to their closest significant pattern.

We extract seasonal patterns from time-series of MOD13 and MOD15 imagery (Tile ID: 51013011, pixel size: 1 km^2). Each Modis image is the composite of the sensor records over 16- (MOD13) and 8-day (MOD15) intervals. Datasets are available from the EOS Data Gateway http://delenn.gsfc.nasa.gov/~imswww/pub/imswelcome/index.html. Detailed accounts of the theoretical basis of both MOD13 and MOD15 and the related algorithms are found in Huete *et al.* (1999, 2002), Knyazikhin *et al.* (1999) and Myneni *et al.* (2002).

We selected time-series covering the period from December 16 /2001 to December 31 /2002, which yielded, for MOD13 and MOD15 datasets respectively, a total of 24 and 48 sequential images per variable. All images were cropped to fit the longitudinal and latitudinal range of the study area and reprojected into the Lat/Lon WGS84 system with the Modis Reprojection Tool (MRT), available from the EROS Data Center's website: http://edcdaac.usgs.gov/landdaac/tools/Modis/index.asp. Images of the MOD13 dataset were also subjected to an image-enhancement procedure in which values from zero to negative were all assigned zero, in order to stress differences among terrestrial areas and to ignore particularities in the spectral responses of permanent water bodies (rivers, lagoons, lakes and the ocean). Thereafter, we calculated the mean value of each image and identified those with abnormally low or high means. These outliers were removed from the datasets.

Functional descriptors and Seasonal Types (STs)

A comprehensive and computationally simple way to trace and recognize significant functional trajectories embodied within the databases, implies a judicious reduction of data variability in time and space, in order to enhance truly ecological heterogeneity while removing as much as possible spurious variation. To do so, we: (1) subset the time-series into seasons and (2) transformed the multi-dimensional and continuous functional heterogeneity, within each seasonal subset, into a multi-state (discrete) variable, each state being a seasonal type (ST). Seasonal subsets contained a maximum of 6 (MOD13) and 12 (MOD15) images per variable, depending on the number of outliers identified previously. The original variables were previously reduced to three descriptive statistics (descriptors) on which we preliminary identified seasonal types in (2).

Functional descriptors should provide a comprehensive characterization of the variables behavior in each MODIS dataset (NDVI and EVI in MOD13, or LAI and FPAR in MOD15). The term 'comprehensive' refers in this context to the readiness of their ecological interpretation and to their ability for rendering a sharp picture of the group-structure of the pixels within each subset. In the case of MOD15 (MODIS LAI and FPAR) dataset, we chose to describe functioning in terms of the seasonal average values of the variables and their interaction, so the seasonal classification of functional entities comprised both the magnitudes of the variables as much as their reciprocal responsiveness. Conversely, the MOD13 (MODIS NDVI and EVI) dataset provided the average, maximum and minimum seasonal values of the Normalize Difference Vegetation Index. The aim was to provide a functional classification that could be at least roughly contrasted with previous typifications of the area, generally based on the NDVI. Using the descriptors as pseudo-bands, independent classifications were performed on MOD13 and on MOD15 to obtain maps of seasonal types, i.e. four maps in a row describing an annual cycle.

Thereafter, the overlaying of consecutive ST classifications allowed the recognition of groups of pixels with identical ST sequences. Groups occupying at least one percent of the study area were regarded as indicators of a meaningful temporal pattern of functioning. These groups define the number of EFTs serving as blueprint for EFT classification. A detailed account of the procedure is found in the following paragraphs.

In symbolic terms, the data element X_{hijk} is the *k*th observation (temporal composite; $k = 1, \ldots, e$; e = up to 6 for MOD13 and up to 12 for MOD15 , depending on the number of removed outliers) taken on MODIS variable j ($j = 1, \ldots, v$ = LAI (L), FPAR (F), NDVI (N)), of pixel i ($i = 1, \ldots, p$) in period h ($h = 1, \ldots, s$). This means that for each pixel i we have s times v e-valued observational vectors. Since we analyze a single annual cycle on a seasonal basis, $s = 4$. Average variables per season (M_{hij}) were obtained for LAI, FPAR and NDVI, according to Equation 1, while the LAI and FPAR observations were paired up to calculate, according to Equation 2, their seasonal interaction (S_{hiLxF}). Other derived descriptors for the NDVI time-series were seasonal maximum (U_{hij}) and seasonal minimum (L_{hij}).

Eq. 1. $M_{hij} = \frac{\left(\sum_{k=1}^{e} X_{hijk}\right)}{e}$ for j = L, F and N

Eq. 2. $S_{hiLxF} = \sum_{k=1}^{e} (X_{hiLk} - M_{hiL})(X_{hiFk} - M_{hiF})$

Henceforth the original seasonal observational vectors gave rise to the descriptor-vectors $\underline{A}_{hi}$ and $\underline{B}_{hi}$, of 3 elements each, as follows:

For MOD15 (LAI/FPAR)

$$\underline{A}_{hi} = \begin{bmatrix} M_{hiL} & M_{hiF} & S_{hiLxF} \end{bmatrix}$$

For MOD13 (NDVI)

$$\underline{B}_{hi} = \begin{bmatrix} M_{hiN} & L_{hiN} & U_{hiN} \end{bmatrix}$$

$\underline{A}_{hi}$ and $\underline{B}_{hi}$ were the components of matrices $\underline{A}_{h}$ and $\underline{B}_{h}$, these later being the set of images collecting the seasonal descriptors of all pixels i in season h. A further step reduced even more the variability of the descriptors by translating the three images per season into a single 8-bit false-color composite (or RGB8). RGB8 data files are simply byte binary files containing color codes (in a 0-215 range) for a specially-encoded color image. They are constructed from three separate images which are assigned to the red, green and blue additive primaries, being the color of each pixel described using only an 8-bit number or color-code. The 8-bit color-code is obtained from linearly rescaling the three images 0 to 5 (integer values only) to later multiply the image in the blue channel by 1, the image in green channel by 6 and the image in the red channel by 36. The color-code is the sum of the products. Further information of this procedure is found in Griffin *et al.* (1992).

Since the color-code assigned to the descriptors could sensibly change the sharpness of the clusters within the RGB8 files, triplets were assigned in every possible combination to the three color channels. To choose among combinations we compared their histograms of frequency and the associated coefficients of variation (CV), assuming that histograms with more defined peaks and lower coefficients identified composites with the sharpest structure of groups. At the conclusion of this stage, each A_{hi} vector had been reorganized and reduced to a C_{hi} scalar containing the 8-bit number associated with the best seasonal RGB8. In a similar manner, B_{hi} had been reduced to D_{hi}.

At the same time, images A_{h} and B_{h} were each used to produce a map of seasonal types (STs) by performing a CLUSTER routine of classification (Eastman 2001). CLUSTER uses a non-hierarchical, histogram peak technique equivalent to looking for the peaks in a n-dimensional histogram, where n is the number of elements in each i-vector and a peak is defined as a value with frequency greater than its neighbors on either side. Divisions between classes fall at the midpoints between peaks and groups with frequencies lower than 1% of the area are disregarded, being their pixels assigned to the closest cluster (Richards 1986).

EFT classifications

The sequence of 8-bit numbers from h = 1, …, 4 (summer to spring), constitutes the vectors C_{i} (MOD15) and D_{i} (MOD13) describing the functional trajectory of pixel i

throughout the annual cycle. Analogously, vectors C_h and D_h represented the images that gathered the 8-bit numbers of all the pixels in season *h*. We converted C_h and D_h into pseudo-bands to feed the EFT's classification routine.

Since $i = 1, \ldots, p$, we also had p T_i vectors containing the sequence of seasonal types for pixel *i*, which were drawn by successively overlying the ST maps. Pixels having identical T_i vectors were pooled into the same class. Classes covering less than 1% of the study area were disregarded. We then examined the quality of the data in the remaining pixel, according to the Quality Assurance Scientific Datasets accompanying the original MOD13 and MOD15 images. Pixels with less than optimal data in 10% or more of the year-long observational vector were also excluded. Further details on the properties and usage of MOD13 and MOD15 Quality Assurance Scientific Datasets can be found in Huete *et al.* (1999) and Myneni *et al.* (2003). The pixels retained for being part of classes larger than one percent of the image and having optimal data in at least 90 percent of the observations, were used to train a routine of Maximum Likelihood Classification (Richards, 1986) based on seasonal 8-bit numbers contained in matrices E_h and F_h.

EFTs, Land-cover types (LCTs) and soils

Since the procedure for classifying EFTs was based on the functional patterns of a single annual cycle, we were interested in testing to what extent the resulting classes mirrored the interplay between the vegetation and its environment. Three criteria were taken into account, according to the tenets we mentioned earlier in this paper: 1- reciprocal coherence between maps obtained from different proxies of ecosystem functioning, in our case NDVI and the interaction between LAI and FPAR. 2- Consistent relationship of the EFT maps with stable, more conservative structural attributes of the regional vegetation types, defined as land-cover types on the basis of dominant physiognomy or land-use traits. For the purpose, we made a land-cover map based on Landsat 7TM and SRTM (topographic) imagery. 3- EFT responsiveness to the spatial arrangement of the regional soils as shown in the General Map of Soils of Rio Grande do Sul (1: 750,000; Streck *et al.* 2002).

Land cover classification based on Landsat TM and SRTM Digital Terrain Model

LANDSAT 7TM bands 3, 4 and 5, covering moisture content, brightness and greenness dimensions, acquired from August to October 2001, were retrieved from http://www.cdbrasil.cnpm.embrapa.br/ (Miranda & Coutinho 2004). The Digital Terrain Model (DTM), modified from that obtained by the Shuttle Radar Topography Mission, was downloaded from the site: http://www.relevobr.cnpm.embrapa.br/ (Miranda 2005). Both types of data were retrieved at a pixel size of 0.0081 km^2 and reprojected to conform the Lat/Lon WGS84 system.

We used the DTM to stratify the study area into three altitudinal belts: 0 –100, 100 – 800 and above 800 m asl, broadly corresponding to the main landscape units. The 0 – 100 belt comprises the coastal plain and the central depression, the 100 – 800 belt encapsulates the Sierra domain and the tablelands domain dominates over the belt above 800 m asl. Landsat bands were sub-divided accordingly and individual classifications performed for each altitudinal belt. On the Landsat data-layers we applied an iterative, self-organizing ISOCLUST routine of classification (Eastman 2001, 2006). ISOCLUST is based on the concept of the widely used ISODATA algorithm (Ball & Hall 1967) in which the pixels are assigned to any of *G* groups following criteria of minimum variance within groups and maximum variance between groups. The number *G* of groups to be produced by the routine is set by the user. A centroid for each group is localized within the *n*-dimensional space defined by the *n* data layers (in this case, Landsat bands) and pixels assigned to the group of the closest centroid. The centroids are recalculated and a new surge of reassignments begins. The routine stops when the centroids remain stable.

Unlike the regular ISODATA procedure, the centroids in the ISOCLUST routine are not seeded at random in the n-dimensional space. Instead, they are located in the center of G groups obtained by a preliminary CLUSTER routine, making so smaller the number of iterations needed to produce stable results. Determining the G number of classes to be produced by the classification is a blind process. We looked for significant breaks of slope in the CLUSTER-produced histogram of frequency (Eastman 2006). The number of classes in the histogram at which each break occurs marks a possible G. We performed classifications for several G values and adopted the land cover map that separated areas recognizably different with greater accuracy.

Classes so-obtained were interpreted in terms of land cover, in accordance with the literature on the subject (FIBGE 1986) and our observations in the field, and assigned any of the following labels: 1- Permanent water body, 2- annual crop (temporally flooded), 3- annual crop, 4- forest plantation, 5- secondary grassland, 6- subtropical grassland (*campo*), 7- grassy wetland, 8- natural forest and 9- shrubland. After overlaying the classifications of the three altitudinal belts to compound a single land-cover map, we checked the accuracy of the map by comparing the predicted land cover distribution with field observations in georeferenced and photographically recorded ground control points.

The Information Theoretical Measure of Interaction between EFTs, LCTs and soils

At this point we have three categorical sets of georeferenced data to be tested for interaction: 1- an EFT classifications accounting for the regional functional heterogeneity, 2- a land-cover classification accounting for structural heterogeneity and 3- a soil classification covering the environmental variability. Categorical data open up the way for an analytical path based on the Information Theory, eliminating so any requirement of normality and linearity constraining the interaction of the entities among and within the datasets (Orlóci 1991). We use the term 'interaction' as a statistical term implying strength in the coherence of objects (classifications) defined in terms of richness and structure. Richness is here the numerousness of the classes in the objects and structure refers to the frequency distribution of individual pixels in the classes (see Orlóci *et al.* 2002).

We use the Renyi's generalized information of order alpha (α), which is a divergence measure on two distributions: P = ($p1, p2, \ldots, p_n$) and Q = ($q1, q2, \ldots, q_n$), being P and Q uniquely paired so that every p_i has a corresponding q_i (Orlóci 1991). For the purposes of this work, we assume that Q is a probability distribution describing the structure of an existing object while P is the probability distribution expected for the object under the null scenario of none structure (i.e. probabilities produced by chance), such as that the Renyi's information contained in a given object is a measure of the departure of its structure from randomness. When α tends to one, Renyi's information takes the form of Kullback's information (2I) shown in Equation 3, in which *N* is the number of observations in P and Q:

Eq. 3. $$2I = 2N\sum_{i=1}^{n} q_i \ln\frac{q_i}{p_i}$$ (Kullback 1968, Orlóci 1991)

In our case, objects under scrutiny are *n*-dimensional contingency tables, with as many dimensions as factors (classifications) sorting the elementary observations (pixels). Association between sorting factors is then, in information terms, a measure of the table's departure from a distribution in which the frequencies of the states in one factor are randomly distributed among the states of the other factors and vice versa. To measure the association between different functional classifications, we produce by crosstabulation a contingency table arranged according to two sorting factors. We consider the taxonomy based on MODIS LAI and FPAR as being sorting factor *R* and the classification based on MODIS NDVI as sorting factor *K*. *R* and *K* have *r* and *k* number of states (classes) respectively. Given the large number of pixels involved leading to enormous differences between the smallest and largest frequencies, we compute interactions from the square root of joint frequencies ($X_{ij} = \sqrt{f_{ij}}$) in order to prevent the largest frequencies from dominating the output of the equations. Symbolizing by X_{ij} the square root of the joint frequency of f_{ij}, in the *ith* LAI/FPAR classification (row) and the *jth* NDVI-classification (column), such that $i = 1, \ldots, r$ and $j = 1, \ldots, k$, the information shared (I_{KxR}) by the functional classifications, as well as the total information they contain (I_{K+R}), is calculated according to Kullback *et al.* (1962) as in equations 4 and 5. Notice that $X_{i\cdot}$ is the marginal sum of the k X_{ij} in the ith row, $X_{\cdot j}$ is the marginal sum of the r X_{ij} in the jth column and N is the overall sum of all the X_{ij} values in the contingency table.

Eq. 4. $$I_{RxK} = \sum_{i=1}^{r}\sum_{j=1}^{k} X_{ij} \ln \frac{N \quad X_{ij}}{X_{i\cdot} \quad X_{\cdot j}}$$

Eq. 5. $$I_{R+K} = \sum_{i=1}^{r}\sum_{j=1}^{k} X_{ij} \ln \frac{X_{ij}}{N/rk}$$

Interaction is then defined in relative terms, ranging from 0 (no interaction) to 1 (maximum interaction) on the basis of I_{RK} and I_{R+K}, as expressed in Coherence Coefficient, C (see Orlóci 1991 and references therein). To determine the probability of having by pure chance a coefficient value as high as the observed, we use random pixel samples and test for sampling sufficiency (Pillar 1998). The C values are calculated for the samples and tested for significance in randomization experiments under the null scenario of a random distribution of NDVI-EFTs among LAI/FPAR-EFTs. Regarding theory and applications we refer to Edgington (1987), Pillar and Orlóci (1996) and Manly (2007) for a systematic account of randomization techniques. Typical to our case, the labels of one functional classification are randomly permuted among pixels while keeping unchanged pixel's identities for the other classification. This method does not modify the specific information of R and K, though it does modify their interaction. Calculations were carried out in a spreadsheet and randomization tests performed using Resampling Stats ©, an add-in for Excel that facilitates bootstrapping, permutation and simulation procedures. We use this package to perform 1,000 randomization steps. After each, the contingency table and all C values are recomputed. We estimate the probability of an at least as extreme C value as the observed $P(C_{(\text{rand})} \geq C)$, by the proportion of randomization-steps scoring values equal to or higher than the observed C. If $P(C_{(\text{rand})} \geq C) < 0.05$

the coherence between R and K is deemed statistically significant at a confidence interval of 0.95.

Regarding the association between the functional classifications, the environmental setting and structural factors of the vegetation, this requires determination of joint frequencies according to three sorting criteria: *H*, *W* and *D*. To that end we perform a cross-tabulation routine and count the number of pixels of each triplet of functional, land-cover and soil typifications. We consider the taxonomy based on functioning as being sorting factor *H,* the classification based on land-covers as sorting factor *W* and the soil classification as sorting factor *D*. *H*, *W* and *D* have *h*, *w* and *d* number of classes respectively. This results in a 3-dimensional contingency table of size *h* x *w* x *d*. As in the case of the interaction between functional classifications, values are subjected to root square transformation ($X_{ijk} = \sqrt{f_{ijk}}$), being X_{ijk} the square root of the joint frequency of the *i*th functional class ($i = 1, \ldots, h$) with the *j*th land-cover type ($j = 1, \ldots, w$) and the *k*th soil type ($k = 1, \ldots, d$).

Questions to be addressed are: 1- What is the information that sorting factor *H* shares with sorting factors *W* and *D* and how much such information represents in quantity compared with the specific information of *H*? This is to ask to what extent the land-cover and soil classifications represent the spatial allocation of factors determining the distribution of the functional types. 2- Is sorting factor *H* equally responsive to sorting factors *W* and *D*, taking *W* and *D* individually? This question aims at comparing the two functional classifications in terms of their sensitiveness to the structural and environmental taxonomies. 3- What is the proportion of the interaction between *W* and *D* that is expressed specifically by *H*? In this case, the question refers to what is the proportion of the response of the land-covers to the environment that is encapsulated by the functional classification. Concerning the first question, the term expressing the joint interaction of *H* with *W* and *D* is $I_{Hx(W+D)}$:

Eq. 6. $$I_{Hx(W+D)}=\sum_{i=1}^{h}\sum_{j=1}^{w}\sum_{k=1}^{d}X_{ijk}\ln\frac{NX_{ijk}}{X_{i\cdot\cdot}\quad X_{\cdot jk}}$$

Where $X_{i\cdot\cdot}$ is the sum of the w x d values in the ith class of H, $X_{\cdot jk}$ is the sum of the h values in the jth class of W and the kth class of D, and N is the overall sum of the values in the three-dimensional contingency table. We express $I_{Hx(W+D)}$ as a fraction of the sum of it-self with the marginal information in H, I_H, being the later measured as shown in equation 7.

Eq. 7. $$I_H=\sum_{i=1}^{h}X_{i}..\ln\frac{X_{i}..}{N/h}$$

The second question requires computation of three information terms: I_{HxW}, I_{HxD} and I_{HxWxD}. The first (Eq. 8) represents the information shared by H and W, without consideration of their interaction joint with factor D. The second term (Eq. 9) ignores the influence of factor W in the interaction between H and D. The third term (Eq. 10) represents the mutual interaction of the three sorting factors, which is a measure of the reciprocal influence of H, W and D one upon the others. The sum of I_{HxW} and I_{HxWxD} provides the overall interaction of the functional and structural classifications. Likewise, the sum of I_{HxD} and I_{HxWxD} provides the overall interaction of the functional and environmental classifications.

Eq. 8. $$I_{HxW}=\sum_{i-1}^{h}\sum_{j=1}^{w}X_{ij}.\ln\frac{NX_{ij}.}{X_{i}..X_{\cdot j}.}$$

Eq. 9. $$I_{HxD}=\sum_{i-1}^{h}\sum_{k=1}^{d}X_{ij}.\ln\frac{NX_{i\cdot k}}{X_{i}..X_{\cdot\cdot k}}$$

Eq. 10. $$I_{HxWxD}=\sum_{i=1}^{h}\sum_{j=1}^{w}\sum_{k=1}^{d}X_{ijk}\ln\frac{X_{ijk}/N}{\left(\dfrac{X_{\cdot jk}\quad X_{i\cdot k}\quad X_{ij\cdot}}{X_{i\cdot\cdot}\quad X_{\cdot j\cdot}\quad X_{\cdot\cdot k}}\right)}$$

The third question, in turn, needs the measurement of yet another term: mutual information between W and D (or I_{WxD}), calculated similarly as shown in equation 11. I_{HxWxD} is then presented as a fraction with I_{WxD}. Notice that the sum of the terms I_{HxWxD}, I_{WxD}, I_{HxD} and I_{HxW} is equal to the total joint information of the three sorting factors, I_{HWD}. A clear picture of the meaning of these information terms is presented in the form of Venn Diagrams in Figure 3. A detailed analysis of information partioning applied to the analysis of the interaction of qualitative, multi-state variables, can be found in Kullback (1968), Orlóci (1978), Orlóci (1991) and Orlóci *et al.* (2002). All the information terms are given in nats and should be divided by ln 2 if translation into bits is needed.

$$\text{Eq. 11. } I_{WxD} = \sum_{j=1}^{w}\sum_{k=1}^{d} X_{\cdot jk} \ln \frac{N X_{\cdot jk}}{X_{\cdot j\cdot} \quad X_{\cdot\cdot k}}$$

As in the case of the interaction between functional classifications, probabilities for the three-way sorting information terms are derived from random samples of pixels, previously tested for sampling sufficiency. Labels of the functional classes are randomly permuted among pixels while keeping unchanged pixel's identities for the land-cover and soil classifications. This is to say that we are not altering the structure of the data related to vegetational or environmental traits, nor the specific information of the functional classification, but merely testing the significance of the spatial association of soil and land-covers with the functional classes. We perform 1,000 randomization steps. After each, the contingency table and all information terms are recomputed. We estimate the probability of an at least as extreme value as the observed $P(I_{(\text{rand})} \geq I)$, by the proportion of randomization-steps scoring values equal to or higher than the observed I. If $P(I_{(\text{rand})} \geq I) < 0.05$, the term is deemed statistically significant at a confidence interval of 0.95.

Although the functional patterns drawn in each classification refer to a unique set of processes connecting the vegetation and the environment, different proxies of functioning may mirror in a different manner the components of the regional vegetation and their association to specific environmental settings. As such, differences among functional classifications may arise from distinctive sensitiveness to certain components. To quantify this in an analysis, we calculated the expected distribution of the land-cover types within the EFTs under a scenario of zero information (land-covers allocated within the functional classes by chance). Thereafter we measured the relative contribution of each land-cover type to the overall divergence between the observed frequencies and those expected in the zero-information scenario. This is to say that we measured the contribution of each land-cover type to the mutual information of the functional and structural taxonomies (I_{HxW}). As land-cover specific contribution to I_{HxW} may change from one environmental setting to another, the analysis was stratified by soil classes, which is to say that we assessed the proportional contribution of each land-cover type to the mutual information conditional to soil classes ($I_{HxW|k}$). Divergences were calculated from the original frequencies, f_{ijk}. Conclusions on the differences between the NDVI- and the LAI/FPAR-based functional classifications were drawn from the comparison of their corresponding outcomes.

RESULTS

LAI / FPAR- and NDVI-based EFT classifications

During the preparation of the time-series, 4 outliers were identified in the MOD15 dataset, which heavily affected the correspondence between FPAR and NDVI. The quality control data, which accompanied each MODIS image, revealed severe atmospheric interferences for the outliers, with cloudiness affecting up to 70% of the area and about 30% of the pixels flagged as having their upwelling reflectances also affected by a high content of aerosols. The removal of these images from the time-series very much improved the performance of the LAI and FPAR in relation to the NDVI. There were not outlier images to be excluded from the MOD13 dataset.

The number of STs per season varied from 9 (summer, winter and spring) to 11 (autumn) when we applied the CLUSTER routine on the descriptors of the MOD15 (LAI / FPAR) dataset, while in the NDVI case the minimum number was 4 STs in winter and the maximum was 7 in spring. Differences in the timing, extension and number of the NDVI- and LAI/FPAR-derived seasonal types (Figures 4 and 5), evidence that differing ways of defining functioning result in different spatio-temporal patterns of functional heterogeneity. As expected, the number and distribution of the ecosystem functional types revealed by the two databases showed remarkable differences. We recognized 12 and 19 EFTs based on NDVI and LAI/FPAR functional parameters, respectively (Figure 6), whose areas and descriptors (means and spatial variability) diverged as shown in Figures 7 and 8.

It should be noticed that greater differences among the average traits of the functional classes in the Lai/Fpar-based classification (M_L, M_F and S_{LxF}) were minimal in summer and maximal during the colder seasons (autumn and winter). On the one hand, the little differences between EFTs in summer may be product of the behavior of the climatic variables during that year, when a moderately dry spell might have constrained the productivity of the more productive types of vegetation, somehow leveling to the low spatial functional variability. On the other hand, greater differences in winter points at temperature (or decaying incoming radiation) as the leading variable triggering the diversity of phenological responses and hence enhancing functional heterogeneity. It might have been particularly so during the abnormally cold winter season of 2002. In a slightly different way, major differences among the NDVI-based EFTs, in terms of the average values of their descriptors M_N, L_N and U_N, were found in winter and spring, which suggests the additional influence of the onset of the growing season on the seasonal performance of the index. Yet, in order to disclose the influence of year-specific climatic patterns it would be necessary to compare our results with those of a different annual cycle, perhaps a La Niña year or any other with the opposite pattern. In the classification based on LAI, FPAR and interaction, EFTs 8 to 12 displayed the largest average LAI and FPAR all throughout the year. Conversely, EFTs 15 to 19 showed the lowest values. There were not clear differences among EFTs in terms of LAI and FPAR interaction (S_{LxF}) since the spatial variability of the parameter was greater within than between classes. Minimum interaction was found in winter and autumn, while maximum values were attained in summer and spring. In the classification based on NDVI, EFTs 8 to 10 were, in average, those reaching highest values of the index, while EFTs 3, 11 and 12 had the least NDVI. EFT 3 also displayed the largest spatial variability of the functional traits.

In the Appendix (Table A1) we give the two-dimensional contingency table resulting from the cross-tabulation of the EFT maps. The Coherence Coefficient showed a numerically strong and highly significant interaction between the NDVI and the LAI/FPAR-derived functional classifications: $C = 0.83$, $P(C_{rand} \geq C) << 0.05$. This outcome supports our tenet that differing ways to characterize ecosystem functioning, though they may produce different pictures of functional heterogeneity in time and space, mirror interconnected processes in a way that the patterns so-described also relate to a high degree one to the other.

Functional classifications and their interaction with land-covers and soils

For the period from August to October of 2001, main land-cover types spread over the area as shown in Figure 9. According to the map, the regional share of land-covers was: 36% for different types of forests (natural forests and plantations included), 35% for grasslands (either natural or secondary), 6% for agricultural areas (including annual and perennial crops), 14% for shrublands and 2% for permanent water-bodies. Due to the effect of topography, about 4% of the study area had abnormally low sensor readings (shaded areas) and was left ignored. A preliminary assessment of the LCT classification accuracy, based on the comparison of the resulting map with georeferenced observations in the field, showed that the classification successfully predicted the occurrence of the land covers about 85% of the cases (in 71 out of 83 ground control points).

From the soils viewpoint, the 60% of the study area corresponds to dystrophic soils of the Inceptisol, Ultisol and Oxisol orders, mostly on top of the old pediplain remnants, while the rest of the area is covered by ill-drained and/or newish eutrophic soils of the Mollisol and Entisol orders (Figure 8). Listed in the Appendix (Tables A2 and A3) are the contingency tables resulting from cross-tabulating each functional classification against the maps of land-covers (background and unclassified pixels excluded) and soil types. In Table 1. we found the information terms, in absolute (nats) and fractional values, concerning the interaction between classifications.

It should be noticed that the taxonomy based on LAI / FPAR, when compared with the NDVI functional classification, has a significantly larger amount of its related information ($I_H + I_{Hx(W+D)}$) due to the interaction with soils and land-covers ($I_{Hx(W+D)}$). However, when marginal information (I_H) is taken into account, the pattern is reversed. This is so because the marginal information of the LAI/FPAR -based taxonomy is twice the same of its NDVI-based counterpart, probably because of its larger richness (19 classes). Regarding the interaction between land-cover and soil types, the share of it encapsulated by the functional classifications is about the same (≈0.15) either using MODIS LAI and FPAR or MODIS NDVI as surrogates of ecosystem functioning. In all cases the probability of having by chance an interaction term as high as the observed is very low ($P(I_{(\mathrm{rand})} \geq I) \ll 0.05$), which points at a minor effect of random and/or year-specific factors on both maps of EFTs. It follows then that we may draw reliable conclusions from the analysis of the contingency tables.

In Figure 10 we present, for the most extensive soil units in the study area, the divergences from random expectation for land-cover frequencies within the functional classes. The magnitudes of the divergences are correlative to the contribution of each land-cover to the mutual information, in each soil unit, between the LCT and the EFT classifications ($I_{HxW|k}$). A detailed analysis of these contributions clearly indicates several things on the nature of the functional entities and its relation with the vegetation: 1- Large divergences within the EFTs are either positive or negative, showing that the functional classes are good predictors of both, the presence and the absence of particular land-covers. We postulate that the larger the divergence of a given LCT within a particular EFT, the more indicative is the EFT on the occurrence of that LCT. In Tables 2 and 3 we present, for each LAI/FPAR and NDVI functional class, the land-cover types better predicted by the EFTs in each soil unit. 2- For a given EFT, the LCTs responsible of the largest positive divergences may change from one soil unit to the next. This implies functional convergences among structurally different classes, dependent on the environmental setting. As such, the meaning of an EFT in terms of land-cover composition strongly depends on what is the soil unit or environmental setting under analysis. 3- Likewise, the same land-cover type may contribute with large, positive divergences to the information specific to different EFTs, manifesting so an important degree of functional heterogeneity within the structural classes. 4- The importance of the land-cover types in determining spatial patterns of functional heterogeneity, depends on how frequent these land-covers are in a given soil unit. On the contrary, the possible influence of rare types of vegetation is largely overridden by their random allocation to several EFTs. It follows from the fact that, when we compare MODIS NDVI and MODIS LAI/FPAR results, in both cases the most frequent land-covers in the *k*th soil unit make the largest contributions to $I_{HxW|k}$. In Tables 4 and 5 we summarize, for the LAI/FPAR and the NDVI-based functional classifications respectively, the land-cover types being large divergence-contributors in each soil class.

The analysis of divergences from random expectation, within the regional units of soils, shows that in most cases a single land-cover type yields more than 50 percent of the negative or positive divergence corresponding to a specific functional class, which clearly associates the EFTs either with the absence and/or with the presence of particular LCTs. Regarding the functional classification based on LAI/FPAR, EFTs displaying larger values of the functional descriptors (EFTs 8 to 12, also with higher values of LAI and FPAR interaction in winter) are in general associated with the presence of natural and commercial forests, as well as with the absence of campos and agricultural areas. This pattern finds its exception in the areas surrounding the coastal lagoons, where these functional units are positively associated with croplands and grasslands. EFTs showing moderately high values of the parameters (EFTs 6 and 7) are positively associated with natural forests over the domain of the *Dystrudepts* and the *Hapludox* and around the coastal lagoons, being also negatively associated to agricultural areas and *campos*. Over the remaining soil domains the pattern is reversed, positively associated with *campos*, commercial forests and croplands, while predicting as well the scarcity of natural forests. A third group of EFTs, with moderate values of the parameters sharply decreasing in winter (EFTs 4, 6, 13 to 17), are characterized by the predominance of campos and the lacking of natural forests. This notwithstanding, in the domain of the *Hapludox*, the EFT 13 is associated with agriculture, most probable of the pomiferous crops. A fourth group is conformed by EFTs 1, 2 and 3, having moderate to low values of the parameters. These are positively related to forest formations only in the domain of the dystrophic Inceptisols and quartzitic Entisols, being in the later probably related to the *restingas*. On the other soil units, this group of EFTs appears positively associated with agricultural areas, grassy wetlands (mainly on the ill-drained *Albaqualf* and *Argiudoll* types) and *campos* on the eutrophic soils of the Sierra domain. The EFTs with lesser seasonal values of LAI, FPAR and interaction (EFTs 18 and 19) are dominated by *campos* and agricultural areas, while are negatively associated with natural forests. In return, in the domain of the *Albaqualfs*, these functional classes are positively associated with commercial forests.

The functional classes derived from MODIS NDVI present as well, in each soil unit, clear correspondence with particular land-cover types. The EFTs with higher values of the index (EFTs 8 to 10) correspond to a great extent to natural forests and forest plantations, also indicating the absence of *campos*. However, in the domain of the eutrophic soils of the Sierra domain, *Argiudolls* and *Udorthents*, these EFTs are dominated by croplands and *campos*. Moderate values of the index, displayed by EFTs 4 to 7, corresponds to natural forests in the domain of the *Dystrudepts* and *Hapludox*, as well as natural forests and commercial forests in the domain of the

Humaquepts. In the areas surrounding the coastal lagoons, these EFTs indicate the presence of *campos*. In the remaining soil units, EFTs 4 and 5 are strongly associated with agricultural areas and *campos*. The lower values of the index, in turn, are displayed by EFTs 1, 2, 3, 11 and 12, being in general positively associated with *campos* and agricultural areas and negatively associated with natural forests.

DISCUSSION

This research is concerned with the classification of the study area into ecosystem functional types. The classification is based on seasonal trajectories of pixels as derived from two different MODIS databases: MOD13 for Spectral Vegetation Indices (SVIs) and MOD15 for LAI and FPAR. The outcomes had to be firstly tested for reliability since there were uncertainties due to the possible inaccuracy of the MODIS sensor records, to the assumptions regarding the vegetation within the MOD15 algorithm (Knyazikhin et al., 1999) and to the relatively short temporal coverage (one annual cycle) of the source data. A further source of error was the changing status of data quality within the images and along the time-series. Any of these uncertainties might cause a certain degree of random allocation of the pixels among the functional classes. If the noise introduced was too severe, the picture of functional heterogeneity so-obtained would lack ecological interpretability.

A straightforward way to test the EFTs was by analyzing their connection with some other functional classifications, with the regional types of vegetation, and with regional soils. In dong this, we assume that ecosystem functioning is a multidimensional, emerging property of the adaptive traits of the vegetation in relation to its biophysical environment. Given its multidimensional nature, ecosystem functioning is definition-dependent, though the many forms it may adopt should certainly be highly interconnected. The spatial heterogeneity of vegetational adaptive traits, in turn, can be broadly represented by a land-cover zonation whose defining criteria are land-use and dominant physiognomy. Likewise, meaningful features of the biophysical environment are encapsulated in, since these are conducive to, the spatial distribution of the soils. We then postulated that the more significant and numerically strong the interaction found, the more reliable the functional zonation of the area.

As seen, all the tested interaction terms are highly unlikely in the null scenario of random sorting, i.e. no association between functional classifications, and between the functional classifications and their structural and environmental counterparts. A Coherence Coefficient of 0.83 amid EFT taxonomies evidence a very high degree of mutuality. This makes every sense given the closely linear relationship between the NDVI and FPAR, and between the NDVI and LAI below NDVI saturation (Broge & Leblanc 2000, Myneni *et al.* 2002). However, the two functional classifications also depart from each other in many aspects, as their differing richness, spatial structure and interaction with the land-cover and soil classifications point out.

A classification based solely on the NDVI defines functional heterogeneity in terms of the available photosynthetically active radiation absorbed by the vegetation cover, which can be readily translated into carbon storage (Running *et al.* 2000). Therefore, the seasonal behavior of the index broadly mirrors the changes throughout the annual cycle of carbon assimilation by the primary producers. Seasonal maxima and minima add evidence on how steady is this process when subjected during the season to events with either positive or negative effect. This is to say that the central criterion to classify pixels into EFTs, when the NDVI is used as surrogate of ecosystem functioning, is carbon assimilation.

In a more complex fashion, a classification based on the seasonal changes of LAI, FPAR and their interaction considers how carbon assimilation responds to the temporal progression of the photosynthetically active biomass of the vegetation. Tracing the joint trajectories of these parameters in terms of seasonal means depicts such a response along the annual cycle. Yet their interaction (S_{LxF}) gives an image of how reactive is one parameter as to the other in shorter periods of time (e.g. one season), and how this reactiveness changes along the year. It follows that the functional taxonomy based on the reciprocal behavior of LAI and FPAR has vegetation phenology as its central classificatory criterion.

That the variation of S_{LxF} within EFTs is larger than between EFTs could discourage the use of this parameter for classification aims. However, it is remarkable that within-class variability greatly changes among the EFTs and that such variability seems to respond to causes other than the frequency of the classes. Larger within-class standard deviations for S_{LxF} (Figure 8) correspond to EFTs 7, 8, 10 and 11, which in neither case are the more extended. This observation calls for a deeper understanding on how, beyond the temporal variability of the response of FPAR to LAI, the spatial heterogeneity of such a response may be indicative of the distribution of distinct functional entities over the study area.

The fact that about 70 percent of the information associated with the LAI/FPAR classification is due to its interaction with soils and land-cover types suggest that the joint behavior of the two functional parameters (i.e. vegetation phenological patterns) largely depends on vegetation physiognomy, land-use and on the set of biophysical factors translated into the nature and distribution of regional soils. Likewise, 77 percent of the information associated with the NDVI classification is explained by the same set of vegetational and environmental factors. This notwithstanding, the functional classifications also present some information that remains unexplained (i.e. marginal information of sorting factor H: I_H). This information certainly accounts for several controls of ecosystem functioning, such as successional dynamics, fire frequency and intensity or disease outbreaks, which are not explicitly considered by broad patterns of land-use, vegetation physiognomy and soil distribution. The fact that the LAI/FPAR-based taxonomy presents almost twice the amount of marginal information than its NDVI-based counterpart, suggests that vegetation phenology is more sensitively an indicator of these controls than carbon assimilation.

In spite of having different values of $I_{Hx(W+D)}$, both functional classifications are almost equivalent in terms of the fraction of the interaction between soils and land-covers, I_{WxD}, in which the functional response is involved ($\frac{I_{HxWxD}}{I_{HxWxD}+I_{WxD}} \approx 0.15$). In both cases the interaction term I_{HxWxD} is relatively small in comparison with I_{WxD}. In the same way, from the interaction between soils and functional units (I_{HxD}) the structural response takes part in a moderate percentage (10 percent when H is the LAI/FPAR taxonomy, and 15 percent when H is the NDVI taxonomy). This notwithstanding, in the two contingency tables under analysis the total interaction term I_{HWD} is large, as well as the interaction terms regarding soils and LCTs (I_{WxD}) and soils and EFTs (I_{HxD}). This is to say that even though there is strong mutuality between the environmental factors and the functional or the structural units, at the regional level, the shape of the response of the functional units to the environment seems to be largely independent of the response of the structural unit to the same set of environmental controls. The relatively small mutuality between LCTs and EFTs, either based on LAI/FPAR or NDVI, (I_{HxW}) points in that direction.

However, when we consider particular units of the regional soils we see a rather high association between functional and structural classes, given that large divergences from random expectation are recurrent for the frequency of the LCTs within the ecosystem functional types (Figure 10, Tables 2 and 3). It follows that the shape of the interaction between ecosystem functioning and vegetation structure is highly dependent on the environmental context. As such, more interpretable trends emerge when the analysis of their reciprocal response is performed in an appropriately constrained environmental space.

There is a general trend of positive association between forest vegetation, mainly natural forests, and the EFTs with largest values of LAI, FPAR and NDVI. Likewise agricultural areas and *campos* tend to be positively associated with the EFTs with lesser values. Nevertheless the relationship between functional classes and land-cover types is largely dependent on what is the soil unit under analysis. Taking the *campos* as an example, we find these dominating the EFTs with moderately high LAI, FPAR and NDVI on the soil units characteristic of the Sierra domain. On the dystrophic soils of the tablelands, in turn, the campos prevail in the EFTs with lesser values of the functional traits. In a similar way, croplands may dominate the LCT composition of the moderately productive EFTs in the valleys of the Sierra domain and in the coastal plain. These observations favor the idea of a rather high functional diversity within the structural classes.

In spite of the clear trends of association between EFTs and LCTs within regional soil units, in neither case the EFTs were occupied by a single land-cover type. Functional convergence between different LCTs certainly accounts for an important part of the structural diversity within the EFTs. However, to a minor extent it might have also arisen from inaccuracies in the source data and from the method we established for EFT recognition. In each step of ST maps overlaying, when we identified groups of pixels to train the maximum likelihood routine of classification, groups of pixels with frequency lower than 1% of the image were excluded. However, in our study area intensive ecosystem transformation and fragmentation have led to a landscape configuration where pixels corresponding to pure stands of either type of land cover have the lesser frequency, generally below 1% of the image. All of these facts end up excluding these areas from our typification. A similar output was described by Paruelo *et al.* (2001) for the temperate region of South America, and by Alcaraz et al. (2006) for the Iberian Peninsula. These authors found a clear correspondence of their functional types of ecosystems with broad bio-geographical units, though those units contained several land use and vegetation types.

It should be mentioned that functional convergences between different LCTs are quite sensible to the use of different surrogates of ecosystem functioning or to any other factor altering the picture of functional heterogeneity drawn by the EFTs. To exemplify the case, we take EFT 8 from the classification based on LAI and FPAR, and EFT 10 from the classification based on NDVI. Notice that these exhibit, all throughout the year, the largest figures of their corresponding functional traits. However, while the functional class identified on the basis of the NDVI shows, in every regional soil unit, a clear positive association with natural forests (see Table 3), the EFT 8 of the Lai/Fpar-based classification is more heterogeneous. It also appears positively associated with commercial forests, croplands and shrublands (Table 2).

It should be mentioned further that, for the results obtained from NDVI, a general agreement exists, in terms of timing and magnitude, with those of previous works in Rio Grande do Sul (Dos Santos & Ferreira 2005, Jacóbsen *et al.*, 2005, Rizzi & Lima da Fonseca, 2001). However, differences regarding the extent of the study area turn out some dissimilar patterns. Previous works have been carried out to the State level, in contrast with the size of the window we analyzed. According to Rizzi & Lima da Fonseca (2001) and Dos Santos & Ferreira (2005), most of the seasonal variability of the index in Rio Grande do Sul responds to the phases of growth and decay of annual crops and grasslands (either natural or secondary), which make altogether about 70% of the vegetation cover in the State (SEMA, on-line). In turn, the functional zonation based on NDVI in our study area, gave major importance to the frequency of natural and commercial forests, *campos* and only secondarily to the agricultural areas (Table 4). In this particular region, natural forests of different sort accounted at the end of 2001 for almost 20 percent of the area, forest plantations did for another 12 percent, about 16 percent was covered by *campos* and croplands made about 18 percent of the extension. In both cases, land-cover types of larger coverage determined to a greater extent the spatial heterogeneity drawn by the index.

FINAL REMARKS

The concept of Ecosystem Functional Types provides a useful tool for depicting the spatial heterogeneity of ecosystem functioning in a given geographic and temporal domain. It captures the most relevant features of the seasonal response of the vegetation to the drivers of the biophysical environment. We have further developed the EFTs, both conceptually and methodologically, to withstand the rapid paces at which spatial patterns of functional heterogeneity may change in response to highly dynamic land-use and climate drivers. Henceforth, the EFTs classified here for the northeastern region of Rio Grande do Sul captured the diversity of functional entities during the annual cycle of 2002.

To analyze how the emerging image of functional heterogeneity responds to different surrogates of ecosystem functioning, we contrasted the EFT maps coming out from 1- the seasonal trajectories of the normalized difference vegetation index (NDVI) and 2- the leaf area index (LAI) in relation to the absorbed photosynthetically-active radiation (FPAR). The resulting maps were undoubtedly coherent and interdependent, given a numerically strong and highly significant information-based coherence coefficient (*C*), as we had anticipated from the interrelated nature of LAI, FPAR and the NDVI. Nonetheless, the two functional maps differed in terms of richness and configuration of their functional entities, as well as in terms of patterns of interaction with a structurally-based land cover classification and the regional distribution of soil types. Being so, functional heterogeneity in the space proved to be heavily dependent on the variables chosen to describe ecosystem functioning. The influence of the different types of vegetation on spatial patterns of functional heterogeneity seems, in turn, to be largely modulated by their frequency: the most frequent a type of vegetation, the higher its influence.

The general picture of ecosystem functioning we have produced, stresses the need of undertaking more detailed analyses of the connection between vegetation types, environmental drivers and EFTs. A more thorough characterization of the vegetation, perhaps including traits indicative of successional stage, land-use strategies or disturbance regime, would certainly helps to understand temporal and spatial patterns of functional heterogeneity. Nevertheless, our analysis has set a basis for more exhaustive studies within the same area and elsewhere.

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Table 1. Information terms regarding the interaction of the functional classifications with the spatial distribution of land-cover and soil types. All the information terms in nats. Notation of the information terms is given in the text. For all terms $P(I_{(\mathrm{rand})} \geq I) << 0.05$

	Lai/Fpar	NDVI
$I_{Hx(W+D)}$	2782	2061
I_H	1198	614
$\frac{I_{Hx(W+D)}}{I_{Hx(W+D)}+I_H}$	0.70	0.77
I_{HxWxD}	212	233
I_{HWD}	4128	3269
I_{WxD}	1346	1207
I_{HxD}	1974	1360
I_{HxW}	596	469
$\frac{I_{HxWxD}}{I_{HxWxD}+I_{WxD}}$	0.14	0.16
$\frac{I_{HxWxD}}{I_{HxWxD}+I_{HxD}}$	0.10	0.15

Table 2. Land-covers (LCTs) better predicted by the LAI/FPAR-based EFTs in each soil unit, according to the divergence of the LCT frequencies from a random distribution within the EFTs. % Div: Divergence as a fraction of the sum of the divergences of the LCTs in each EFT, in the corresponding soil unit. In **bold**, fractions larger than 0.5, pointing at a strong predictability of the EFT on the presence of the absence of the land-covers. When the divergence is positive, the EFT predicts land-cover presence, otherwise the EFT predicts land-cover absence. LCTs are: **NF** – Natural forest, **CF** – Commercial forest, **Ca** – *Campo*, natural grassland, **SG** – Secondary grassland, **GW** – Grassy wetland, **Shr** – Shrubland, **WB** – permanent water body, **Cr** – Cropland, with growing crop, **Cr(fld)** –cropland, temporally flooded, **Br/ur** – Tilled soil and urban.

Lai/Fpar	Hapludult				Dystrudept				Argiudoll				Humaquept				Shore / lakes			
EFT	Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative	
	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT
1	0.34	Ca	**0.84**	SG	**0.58**	CF	0.50	Ca	0.30	Ca	0.43	CF	**0.63**	Br/Ur	0.34	NF	0.37	Ca	0.28	GW
2	0.41	Cr	0.49	NF	**0.81**	NF	0.49	GW	**0.51**	GW	**0.78**	NF	0.43	CF	**0.52**	NF	**0.57**	NF	0.34	Cr
3	0.36	Ca	**0.73**	NF	0.38	GW	**0.72**	CF	**0.57**	GW	**0.88**	NF	0.44	Br/Ur	0.39	SG	**0.62**	NF	0.34	SG
4	0.22	WB	**0.54**	NF	**0.56**	Ca	**0.53**	NF	0.25	WB	**0.70**	NF	0.25	Shr	0.48	Br/Ur	0.21	WB	**0.78**	NF
5	0.22	WB	**0.54**	NF	**0.70**	Ca	**0.59**	NF	0.25	WB	**0.70**	NF	0.25	Shr	0.48	Br/Ur	0.21	WB	**0.78**	NF
6	**0.73**	Ca	**0.62**	NF	**0.64**	NF	**0.68**	Ca	0.40	Cr	**0.63**	NF	**0.61**	CF	0.34	NF	**0.52**	NF	0.32	Cr
7	**0.58**	Cr	**0.68**	Ca	**0.64**	NF	**0.62**	Ca	0.38	Cr	0.40	SG	0.31	Cr(fld)	**0.65**	Br/Ur	**1.00**	NF	0.33	Ca
8	**0.56**	NF	**0.80**	Ca	**0.58**	CF	**0.56**	Ca	0.48	CF	0.42	Cr	**0.51**	NF	0.41	Cr(fld)	**0.91**	Cr	**0.62**	NF
9	**0.74**	NF	**0.59**	Ca	**0.57**	CF	**0.62**	Ca	**0.57**	NF	0.33	GW	0.45	NF	0.41	Br/Ur	**0.91**	SG	0.36	Cr
10	**0.93**	NF	**0.70**	Ca	**0.52**	CF	**0.63**	Ca	0.36	NF	**0.65**	CF	**0.53**	Cr	0.50	Br/Ur	**0.92**	Cr	0.23	Shr
11	**0.98**	NF	0.30	Cr	**0.53**	CF	**0.59**	Ca	**0.74**	NF	0.36	GW	**0.87**	CF	0.49	Cr(fld)	0.23	WB	**0.60**	NF
12	**0.73**	NF	**0.57**	Ca	0.50	CF	**0.65**	Ca	**0.81**	NF	0.35	GW	0.41	Cr	**0.54**	Br/Ur	**0.82**	NF	0.38	Cr
13	0.30	SG	**0.65**	NF	**0.56**	NF	0.50	CF	0.39	Cr(fld)	**0.89**	NF	0.41	CF	**0.53**	NF	0.23	WB	**0.60**	NF
14	0.38	SG	**0.81**	NF	**0.58**	GW	**0.64**	CF	0.38	GW	**0.92**	NF	**0.53**	CF	0.50	NF	0.21	WB	**0.78**	NF
15	0.22	WB	**0.54**	NF	**0.80**	Ca	**0.56**	NF	0.34	CF	**0.56**	NF	0.44	Cr(fld)	**0.71**	Br/Ur	0.21	WB	**0.78**	NF
16	**0.57**	Ca	**0.85**	NF	**0.72**	Ca	**0.52**	NF	**0.57**	SG	**0.56**	NF	**0.62**	CF	0.40	Br/Ur	0.21	WB	**0.78**	NF
17	0.29	Ca	**0.96**	NF	**0.70**	Ca	**0.52**	NF	0.40	Br/Ur	**0.83**	NF	0.25	Shr	0.48	Br/Ur	0.21	WB	**0.78**	NF
18	**0.71**	Ca	**0.85**	NF	**0.84**	Ca	**0.53**	NF	0.38	Br/Ur	**0.71**	NF	**0.69**	Br/Ur	0.36	NF	0.21	WB	**0.78**	NF
19	0.41	Ca	**0.94**	NF	0.36	Cr	0.37	SG	**0.52**	Cr(fld)	0.39	NF	**0.51**	Br/Ur	0.39	CF	0.21	WB	**0.78**	NF

Lai/Fpar	Hapludox				Eutr. Udorthent				Albaqualf				Argiudoll / Eutr.Udorthent				Dyst.Udorthent / Humaquept			
EFT	Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative	
	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT	Div %	LCT
1	**0.75**	Cr	**0.79**	Ca	**0.71**	Br/Ur	0.46	Ca	0.49	Br/Ur	**0.71**	SG	**0.69**	Ca	0.50	CF	0.39	SG	**0.58**	Shr
2	0.49	Shr	**0.67**	Ca	0.49	NF	**0.61**	Br/Ur	**0.53**	GW	0.35	Ca	**0.60**	Ca	0.45	NF	0.30	Ca	**0.66**	NF
3	0.35	NF	**0.51**	Ca	0.39	Ca	**0.56**	Br/Ur	0.39	NF	**0.51**	CF	**0.60**	Ca	**0.53**	NF	**0.77**	Ca	**0.67**	NF
4	**0.94**	Ca	0.43	NF	0.49	Shr	0.41	Br/Ur	**0.80**	CF	0.36	Cr	0.23	WB	**0.65**	NF	0.22	WB	**0.82**	NF
5	**0.90**	Ca	0.32	Cr	0.49	Ca	0.35	NF	**0.74**	CF	0.42	Cr	0.34	Shr	**0.73**	NF	0.22	WB	**0.82**	NF
6	0.42	NF	**0.70**	Ca	0.34	Br/Ur	**0.61**	Ca	0.44	SG	**0.53**	CF	**0.62**	Ca	0.47	NF	**0.55**	Ca	**0.79**	NF
7	**0.52**	NF	**0.78**	Ca	**0.72**	NF	0.50	Br/Ur	0.37	Ca	**0.62**	CF	**0.58**	Ca	0.45	NF	**0.78**	Ca	**0.68**	NF
8	0.32	SG	0.50	Shr	0.43	Br/Ur	0.38	Ca	0.48	CF	0.38	SG	**0.68**	CF	0.40	Ca	**0.63**	Shr	0.37	NF
9	0.45	NF	**0.82**	Ca	0.49	NF	0.43	Ca	0.25	NF	**0.59**	CF	**0.66**	NF	**0.71**	Ca	**0.91**	NF	**0.54**	Ca
10	**0.54**	NF	**0.63**	Ca	**0.59**	NF	0.34	Ca	**0.64**	NF	**0.63**	CF	0.43	Ca	**0.51**	CF	**0.52**	Shr	0.31	Cr
11	0.48	CF	**0.74**	Ca	**0.61**	NF	0.44	Ca	**0.58**	NF	0.45	CF	**0.61**	NF	0.49	CF	0.46	NF	**0.58**	Ca
12	0.44	NF	**0.68**	Ca	**0.66**	CF	**0.67**	Ca	0.47	Ca	**0.54**	CF	**0.69**	NF	0.43	CF	**0.93**	NF	**0.70**	Ca
13	**0.57**	Cr	**0.59**	Ca	0.35	Ca	0.47	Br/Ur	0.40	SG	0.35	CF	**0.61**	Ca	**0.57**	NF	**0.55**	Ca	**0.64**	NF
14	0.46	Shr	0.50	Cr	0.39	Br/Ur	**0.53**	Shr	**0.69**	SG	**0.62**	CF	0.44	Ca	**0.85**	NF	0.25	Shr	**0.84**	NF
15	**1.00**	Ca	0.31	Cr	**0.70**	Ca	0.32	Br/Ur	**0.77**	CF	0.37	Cr	**0.58**	Ca	**0.56**	NF	0.22	WB	**0.82**	NF
16	**1.00**	Ca	0.32	Cr	**0.62**	Ca	0.37	NF	**0.63**	SG	0.44	Br/Ur	**0.56**	Ca	0.40	CF	0.22	WB	**0.82**	NF
17	**0.83**	Ca	**0.60**	Cr	**0.69**	Ca	0.33	NF	0.30	Shr	**0.52**	CF	0.22	WB	**0.81**	NF	0.22	WB	**0.82**	NF
18	**0.54**	Ca	0.48	NF	0.43	Ca	**0.61**	NF	**0.79**	CF	0.41	SG	0.45	Ca	**0.59**	NF	0.22	WB	**0.82**	NF
19	**0.98**	Cr	0.43	Ca	0.40	Br/Ur	0.45	Ca	**0.58**	CF	0.41	SG	0.22	WB	**0.81**	NF	**0.61**	Cr	**0.66**	NF

Table 3. Land-covers (LCTs) better predicted by the LAI/FPAR-based EFTs in each soil unit, according to the divergence of the LCT frequencies from a random distribution within the EFTs. % Div: Divergence as a fraction of the sum of the divergences of the LCTs in each EFT, in the corresponding soil unit. Divergences and LCT labels as in Table 2.

NDVI	Hapludult				Dystrudept				Argiudoll				Humaquept				Shore / lakes			
EFT	Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative	
	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT
1	0.36	CF	**0.56**	NF	0.37	SG	**0.76**	CF	0.49	GW	**0.53**	NF	**0.59**	Cr(fld)	0.39	Br/Ur	0.45	NF	0.31	Cr
2	0.41	Ca	**0.80**	NF	0.30	Ca	0.49	NF	0.36	GW	**0.91**	NF	0.34	GW	0.47	NF	0.23	WB	0.37	NF
3	0.43	Cr	**0.79**	NF	**0.62**	NF	0.44	Ca	0.33	Cr(fld)	0.47	NF	**0.85**	Br/Ur	0.38	Cr	0.44	CF	0.40	NF
4	**0.57**	Cr	0.40	Ca	**0.68**	NF	**0.63**	Ca	**0.95**	Cr	**0.56**	CF	0.49	Cr	0.46	Br/Ur	**0.83**	Cr	0.34	NF
5	**1.00**	Ca	**0.53**	SG	**0.65**	NF	**0.66**	Ca	0.46	Cr	**0.51**	NF	0.46	Cr	0.44	Br/Ur	0.37	NF	0.50	Br/Ur
6	0.41	NF	**0.64**	Ca	**0.80**	NF	0.46	Ca	**0.54**	Cr	0.39	NF	**0.78**	NF	0.42	Cr	0.37	Ca	0.31	Br/Ur
7	0.48	Ca	**0.76**	NF	**0.66**	NF	0.41	Ca	0.42	Cr	**0.69**	NF	**0.81**	CF	**0.66**	NF	0.32	SG	0.47	Br/Ur
8	**0.82**	NF	0.45	Cr	**0.82**	CF	**0.57**	Ca	**0.55**	NF	0.39	Cr	**0.68**	NF	**0.55**	Br/Ur	0.23	WB	0.37	NF
9	**1.00**	NF	0.32	SG	**0.57**	NF	**0.62**	Ca	0.49	NF	0.45	CF	0.36	Cr	**0.53**	Br/Ur	**0.56**	NF	0.37	Cr
10	**0.72**	NF	**0.63**	Ca	**0.58**	CF	**0.63**	Ca	**0.63**	NF	0.42	Cr	**0.61**	NF	**0.53**	Br/Ur	**0.73**	NF	0.38	Cr
11	0.37	Ca	**0.91**	NF	**0.70**	Ca	**0.57**	NF	**0.51**	Cr	**0.90**	NF	**0.70**	CF	0.46	NF	0.49	Br/Ur	0.50	NF
12	0.35	CF	**0.75**	NF	**0.74**	Ca	0.46	NF	**0.57**	Ca	**0.78**	NF	**0.53**	Br/Ur	0.35	NF	**0.73**	Br/Ur	**0.59**	NF

NDVI	Hapludox				Eutr. Udorthent				Albaqualf				Arg-oll / E. Ud-nt				D.Ud-nt / Hum-ept			
EFT	Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative	
	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT	% Div	LCT
1	**0.68**	NF	**0.57**	Cr	0.38	Ca	**0.51**	Br/Ur	**0.53**	Cr(fld)	0.28	SG	**0.53**	Ca	0.46	NF	0.35	Ca	**0.75**	NF
2	**0.59**	Shr	**0.76**	Cr	**0.68**	Ca	0.42	Br/Ur	**1.00**	SG	0.39	Cr	**0.53**	Ca	**0.65**	NF	**0.56**	Ca	**0.77**	NF
3	**1.00**	Cr	0.36	NF	**0.79**	Br/Ur	0.36	NF	**0.66**	CF	0.35	SG	0.44	Br/Ur	**0.76**	NF	**0.59**	Cr	0.44	NF
4	0.50	NF	**0.70**	Ca	**0.60**	NF	**0.68**	Br/Ur	0.41	NF	0.38	CF	0.49	Ca	**0.65**	NF	**0.65**	Ca	**0.92**	NF
5	**0.54**	NF	**0.69**	Ca	**0.61**	Cr	0.49	Ca	0.47	NF	**0.58**	CF	0.40	Br/Ur	**0.72**	NF	**0.55**	Ca	0.35	SG
6	**0.53**	NF	**0.66**	Ca	0.39	NF	**0.52**	Br/Ur	0.48	NF	0.42	CF	**0.59**	Ca	**0.52**	NF	**0.54**	Ca	**0.69**	NF
7	0.48	NF	**0.64**	Ca	0.43	Br/Ur	0.38	Ca	**0.59**	SG	**0.62**	CF	**0.53**	Ca	**0.63**	NF	**0.67**	Ca	**0.66**	NF
8	0.37	CF	**0.71**	Ca	**0.67**	NF	0.47	Ca	0.46	Ca	0.40	Cr	**0.53**	Cr	0.40	Shr	**0.52**	NF	**0.51**	Shr
9	0.43	NF	**0.75**	Ca	**0.77**	NF	**0.52**	Br/Ur	**0.79**	NF	**0.62**	CF	**0.83**	Ca	0.41	CF	**1.00**	Ca	0.45	Shr
10	0.48	NF	**0.70**	Ca	0.49	NF	0.31	Br/Ur	**0.72**	NF	0.41	CF	**0.61**	NF	**0.55**	Ca	**0.73**	NF	**0.71**	Ca
11	**0.96**	Ca	0.42	Cr	**0.59**	Ca	**0.57**	NF	0.42	CF	**0.52**	SG	**0.59**	Br/Ur	**0.61**	NF	0.49	Cr	**0.63**	NF
12	**0.55**	Ca	0.46	NF	**0.82**	Br/Ur	**0.65**	NF	**0.63**	CF	0.44	SG	0.48	Br/Ur	**0.66**	NF	**0.65**	Cr	0.40	NF

Table 4. Contribution of the land-cover types to the mutual information between the functional (LAI/FPAR-based) and structural classifications in each *k*th soil unit ($I_{HxW|k}$). Contribution as a fraction of the sum of the divergences from random expectation. In **bold**, higher contributions per soil type. See Table 2 for land-cover types notation.

Regional soil type	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur
Positive contributions of the LCTs to IHxW!k										
Hapludult	0.00	0.01	0.10	0.06	0.10	**0.26**	0.04	**0.36**	0.04	0.03
Dystrudept	0.00	0.00	0.02	**0.22**	0.05	**0.33**	0.11	**0.22**	0.05	0.00
Argiudoll	0.00	0.05	0.12	0.12	0.06	0.07	**0.17**	**0.29**	0.04	0.07
Humaquept	0.00	0.04	**0.50**	0.16	0.05	0.00	0.03	0.14	0.00	0.07
Hapludox	0.00	0.00	0.13	0.09	0.04	**0.36**	0.03	0.15	0.11	0.09
Eutr.Udorthent	0.00	0.01	0.04	0.13	0.02	**0.27**	0.08	**0.21**	0.11	0.12
Albaqualf	0.01	0.03	0.09	**0.27**	0.24	0.11	0.06	0.11	0.01	0.09
Lagoon shores	0.01	0.01	0.02	0.00	0.02	**0.61**	0.07	0.04	0.19	0.03
Argiudoll/Eutr.Udorthent	0.00	0.00	0.10	**0.23**	0.08	0.19	0.03	**0.23**	0.11	0.02
Dyst.Udorthent /Humaquept	0.02	0.02	0.06	0.07	0.05	**0.27**	0.04	**0.34**	0.12	0.02
Negative contributions ...										
Hapludult	0.00	-0.01	-0.10	-0.06	-0.10	**-0.26**	-0.04	**-0.36**	-0.04	-0.03
Dystrudept	0.00	0.00	-0.02	**-0.26**	-0.04	**-0.29**	-0.10	**-0.24**	-0.05	0.00
Argiudoll	0.00	-0.04	**-0.15**	-0.10	-0.05	-0.09	**-0.16**	**-0.32**	-0.04	-0.05
Humaquept	0.00	-0.08	-0.05	-0.06	-0.05	**-0.44**	-0.06	-0.05	-0.06	-0.14
Hapludox	0.00	0.00	**-0.21**	-0.10	-0.03	**-0.32**	-0.04	-0.18	-0.13	0.00
Eutr.Udorthent	-0.01	-0.01	-0.06	**-0.15**	-0.06	**-0.17**	-0.05	**-0.17**	-0.06	-0.25
Albaqualf	-0.01	-0.03	-0.07	**-0.31**	-0.16	-0.10	-0.05	-0.12	-0.01	-0.14
Lagoon shores	0.00	0.00	**-0.22**	**-0.45**	-0.14	-0.01	0.00	-0.15	-0.01	-0.01
Argiudoll/Eutr.Udorthent	0.00	0.00	-0.07	-0.19	-0.06	**-0.25**	-0.04	**-0.22**	-0.14	-0.02
Dyst.Udorthent /Humaquept	-0.02	-0.02	-0.08	-0.07	-0.08	**-0.28**	-0.03	**-0.35**	-0.07	-0.02

Table 5. Contribution of the land-cover types (columns) to the mutual information between the functional (NDVI-based) and structural classifications in each *k*th soil unit ($I_{HxW|k}$). Contribution as a fraction of the sum of the divergences from random expectation. In **bold**, higher contributions per soil type. See Table 2 for land-cover types notation.

Regional soil type	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Agr/Ur
Positive contributions of the LCTs to IHxW!k										
Hapludult	0.02	0.04	0.10	0.07	0.08	0.15	0.11	**0.25**	0.10	0.08
Dystrudept	0.01	0.02	0.05	**0.27**	0.05	**0.21**	0.15	0.18	0.05	0.01
Argiudoll	0.02	0.10	0.11	0.10	0.07	0.12	0.10	**0.22**	0.09	0.08
Humaquept	0.03	0.08	0.14	0.14	0.14	0.02	0.08	0.16	0.02	**0.18**
Hapludox	0.01	0.01	**0.23**	0.15	0.06	**0.24**	0.06	0.16	0.07	0.01
Udorthent Eutrophic	0.03	0.09	0.10	0.09	0.03	0.10	0.05	0.17	0.11	**0.23**
Albaqualf	0.04	0.05	0.08	**0.18**	0.16	0.12	0.05	0.14	0.04	0.14
Lagoon shores	0.05	0.08	0.13	0.11	0.07	0.13	0.09	0.12	0.07	**0.15**
Argiudoll/Eutr.Udorthent	0.04	0.05	0.07	0.08	0.09	0.13	0.07	**0.20**	0.08	0.18
Dyst.Udorthent /Humaquept	0.06	0.06	0.15	0.12	0.10	0.14	0.04	**0.19**	0.07	0.06
Negative contributions ...										
Hapludult	-0.02	-0.04	-0.10	-0.07	-0.08	-0.15	-0.11	**-0.25**	-0.10	-0.08
Dystrudept	-0.01	-0.01	-0.05	**-0.24**	-0.07	**-0.23**	-0.15	-0.18	-0.06	-0.01
Argiudoll	-0.02	-0.10	-0.11	-0.12	-0.07	-0.08	-0.13	**-0.18**	-0.08	-0.10
Humaquept	-0.03	-0.12	**-0.18**	-0.12	-0.11	-0.03	-0.07	-0.15	-0.03	-0.16
Hapludox	-0.01	-0.02	**-0.23**	-0.16	-0.06	**-0.20**	-0.05	-0.15	-0.05	-0.06
Udorthent Eutrophic	-0.02	-0.06	-0.08	-0.07	-0.05	-0.15	-0.08	**-0.19**	-0.13	-0.18
Albaqualf	-0.04	-0.08	-0.08	**-0.18**	-0.15	-0.10	-0.05	-0.15	-0.04	-0.13
Lagoon shores	-0.05	-0.03	-0.15	**-0.18**	-0.08	-0.08	-0.04	-0.18	-0.07	-0.14
Argiudoll/Eutr.Udorthent	-0.04	-0.06	-0.07	-0.07	-0.08	-0.15	-0.08	**-0.20**	-0.08	-0.18
Dyst.Udorthent /Humaquept	-0.07	-0.07	-0.12	-0.11	-0.11	-0.15	-0.07	**-0.16**	-0.07	-0.07

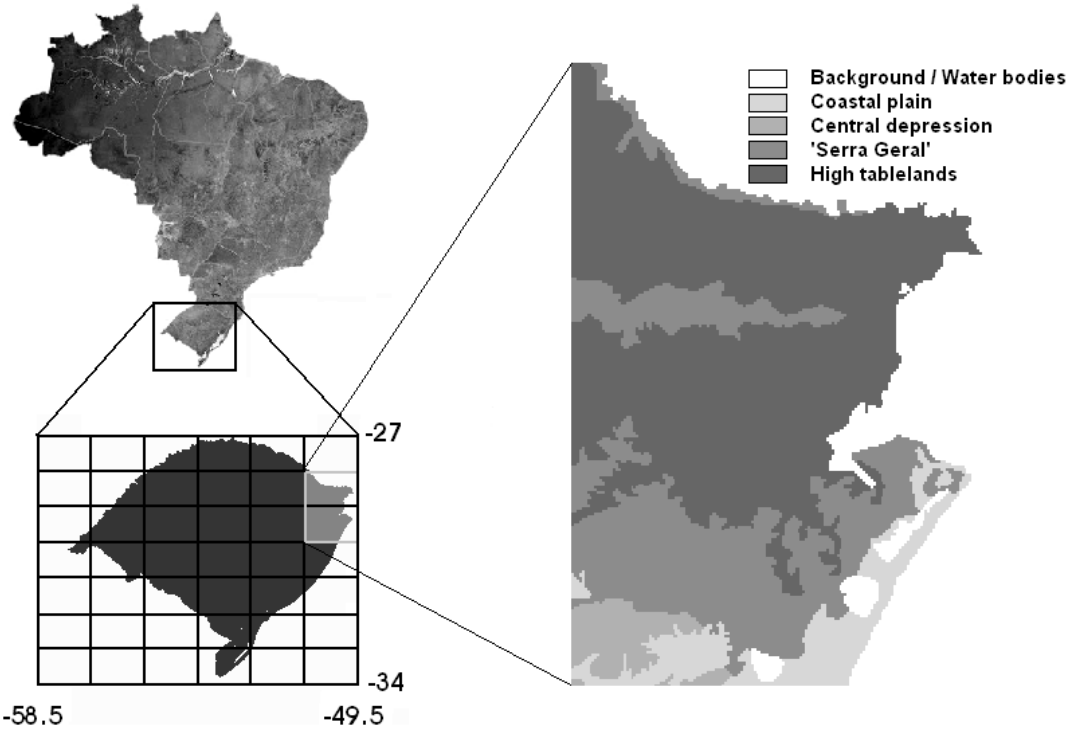

Figure 1. A- The location of the study area. Grid in lower-left panel in geographical coordinates. B- Distribution of the major landscape types in the study area, derived from the interpretation of local soil units as they appear in Streck *et al.* (2002).

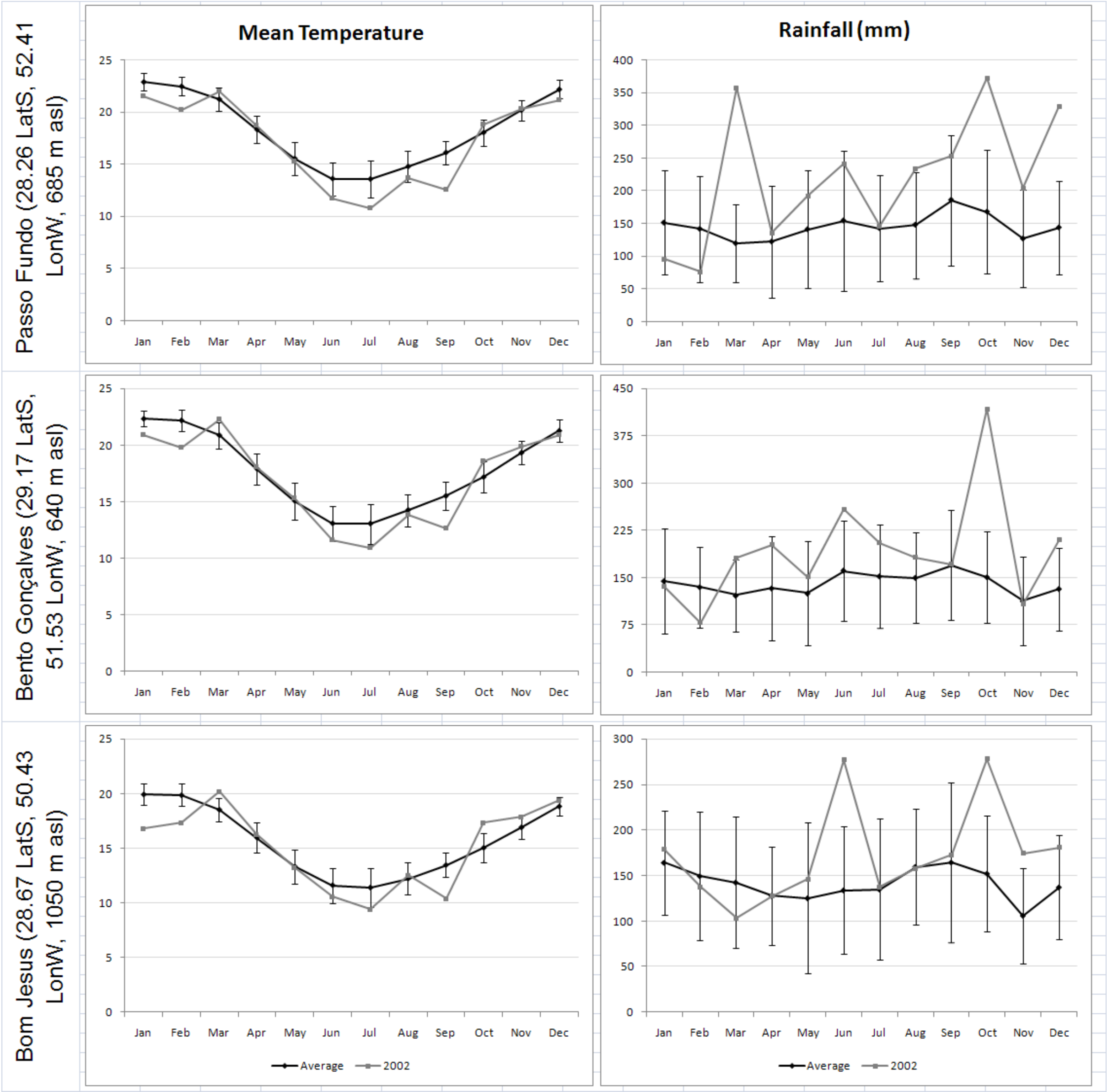

Figure 2. Mean temperature (°C) and rainfall (mm) in three climatic stations within or near the study area. Location and altitude of the stations have been placed to the left of the graphic boxes. The error bars around each historical monthly mean (average) represent the corresponding standard deviation.

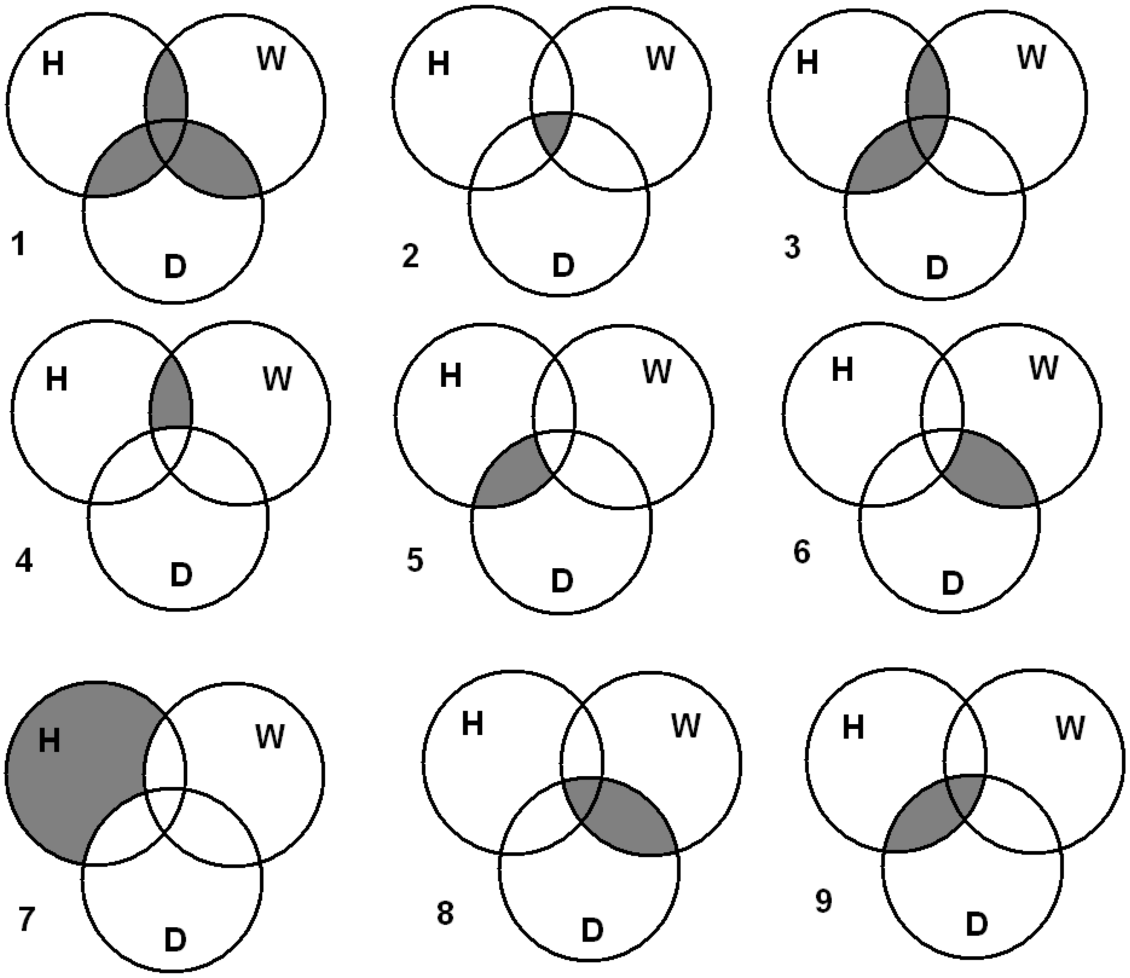

Figure 3. Venn Diagrams representing some critical information terms in three-dimensional contingency tables. 1- Thee-way joint interaction, I_{HWD}. 2- Mutual interaction, I_{HxWxD}. 3- Joint interaction of H with W and D, $I_{Hx(W+D)}$. 4- Marginal interaction of H and W, I_{HxW}. 5- Marginal interaction of H and D, I_{HxD}. 6- Marginal interaction of W and D, I_{WxD}. 7- Marginal information of H, I_H. 8- Joint interaction of W and D, conditional on H, $I_{WxD|H}$. 9- Joint interaction of H and D, conditional on W, $I_{HxD|W}$.. Notice that some of these terms (1, 3, 8 and 9) are decomposable into several of the others. For instance the term in number 8, $I_{WxD|H}$, equals the sum of I_{WxD} and I_{HxWxD}. Likewise, the term in 9, $I_{HxD|W}$, equals the sum of I_{HxD} and I_{HxWxD}. After Orlóci *et al.* 2002.

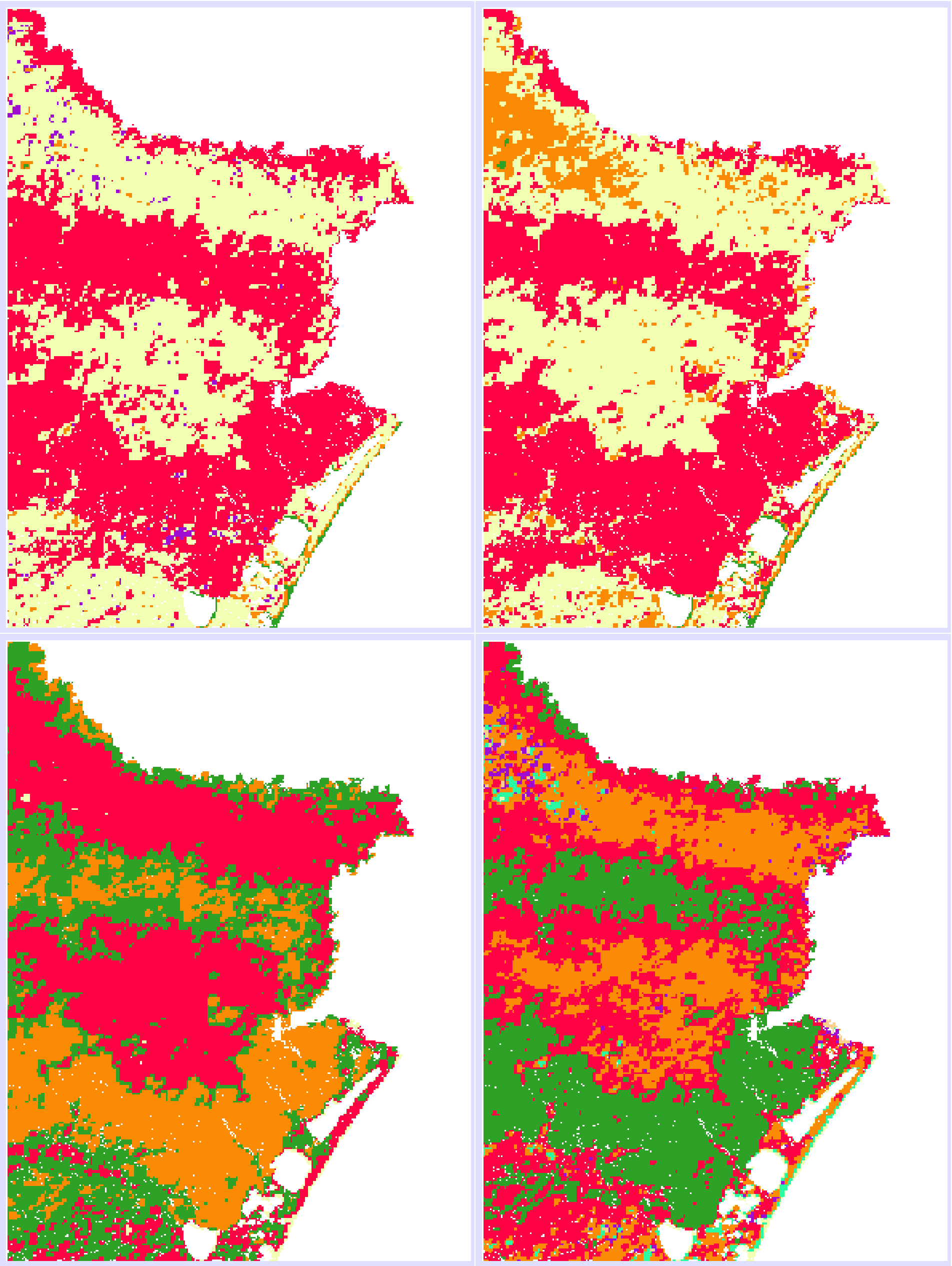

Figure 4. NDVI-based ST maps. From upper left to lower right: Summer (5 STs), autumn (5), winter (4) and spring (7).

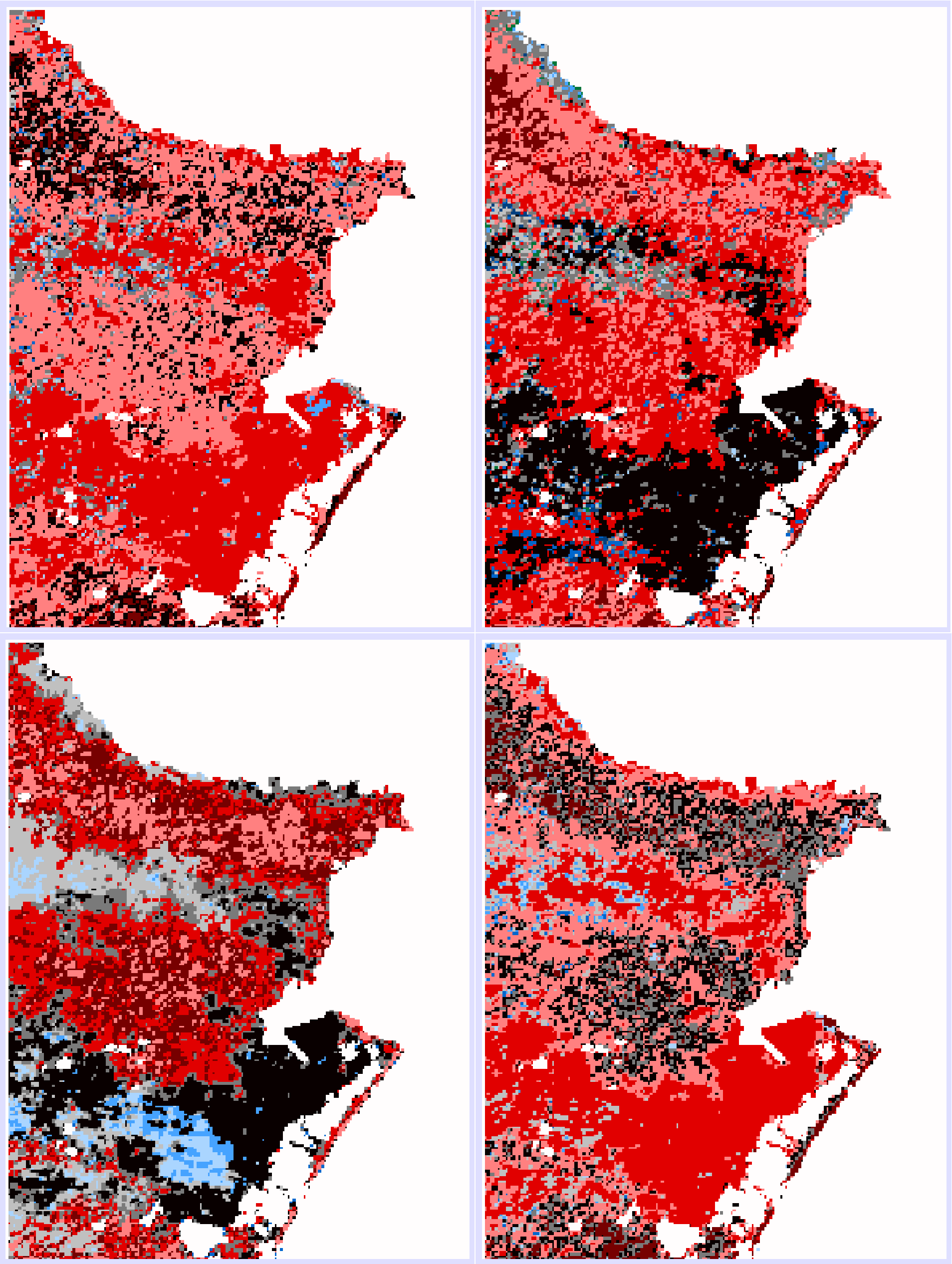

Figure 5. LAI/FPAR-based ST Maps. From upper left to lower right: Summer (9STs), autumn (11), winter (9) and spring (9).

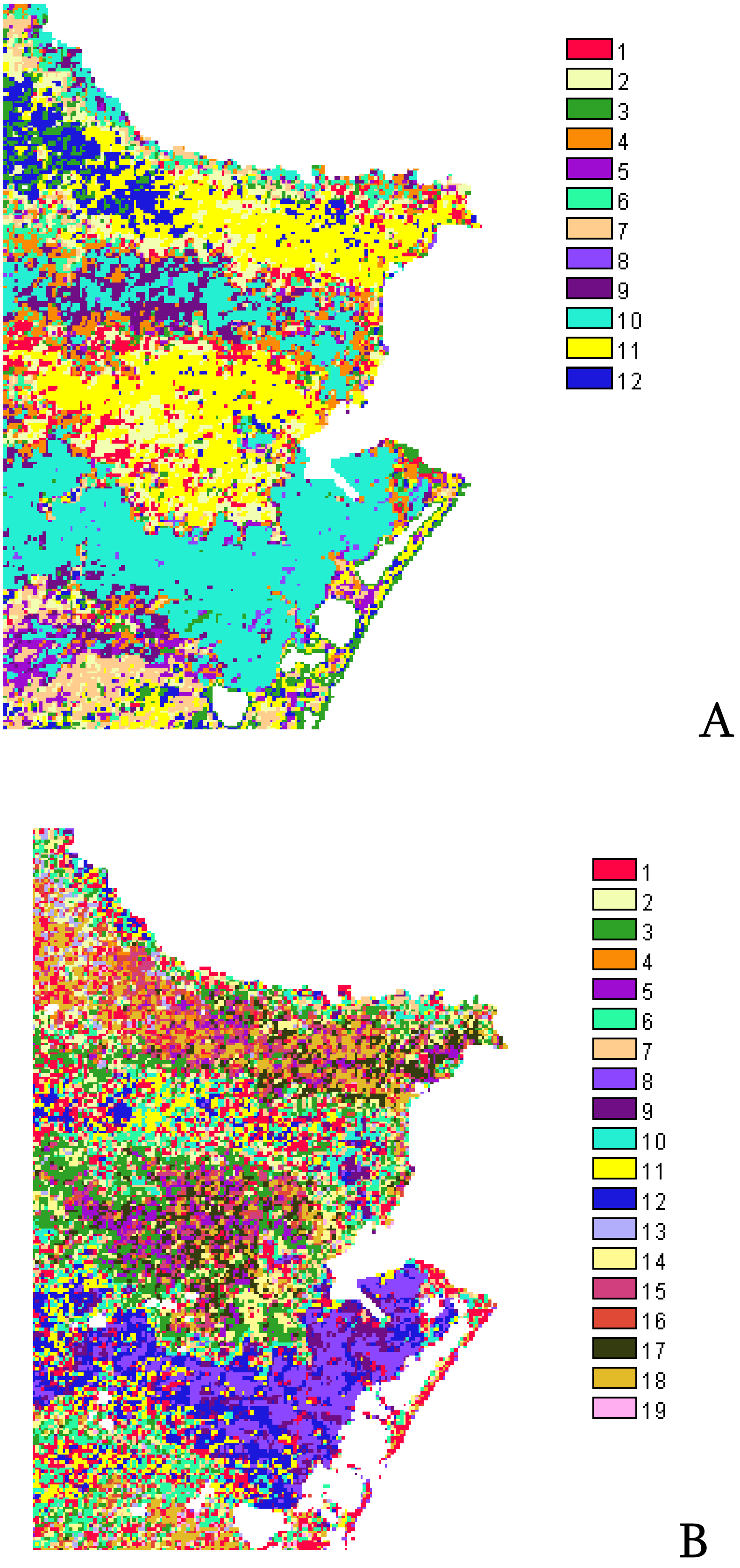

Figure 6. Panel A- NDVI-based Ecosystem Functional Types. 12 classes, pixel size: 1 km^2. Panel B- LAI/FPAR-based Ecosystem Functional Types. 19 classes, pixel size: 1 km^2.

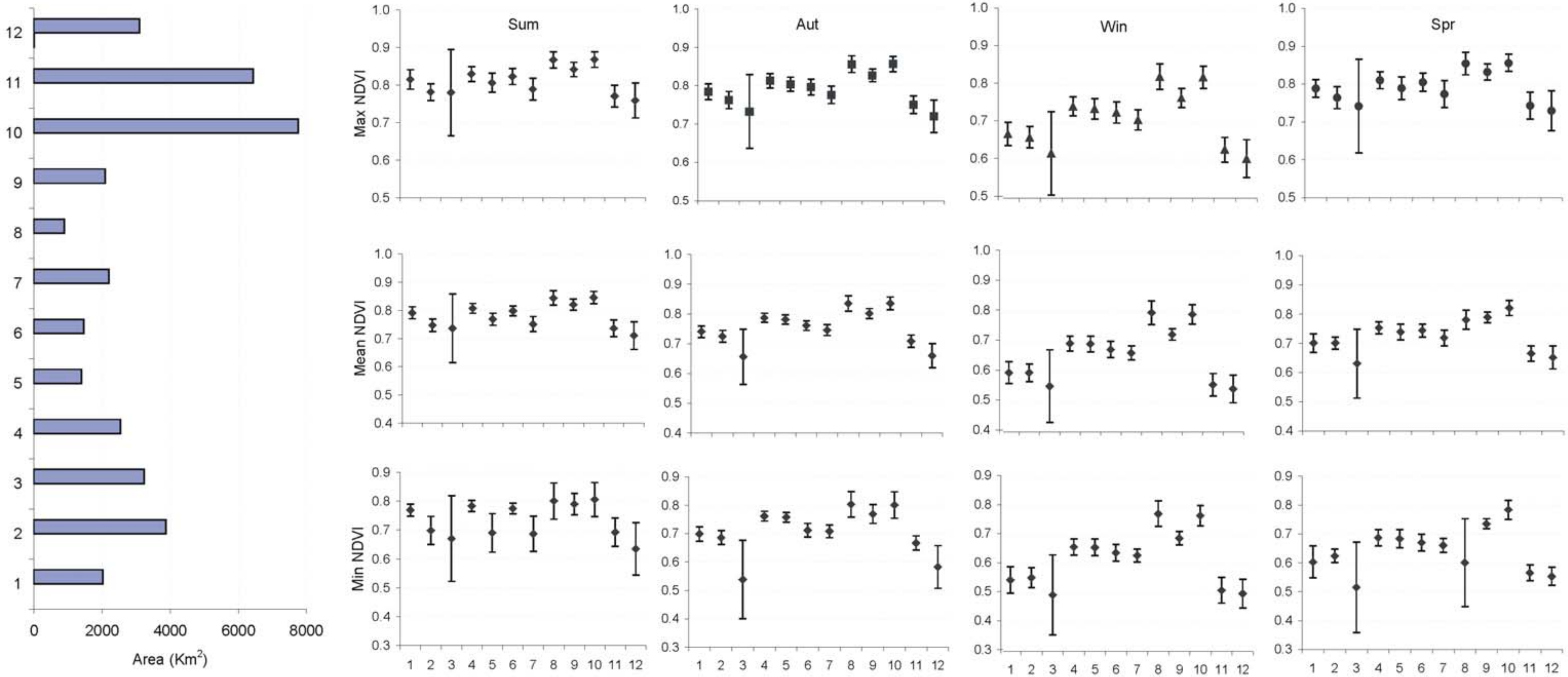

Figure 7. Area and seasonal descriptors (means ± SD) of the 12 NDVI-based Ecosystem Functional Types.

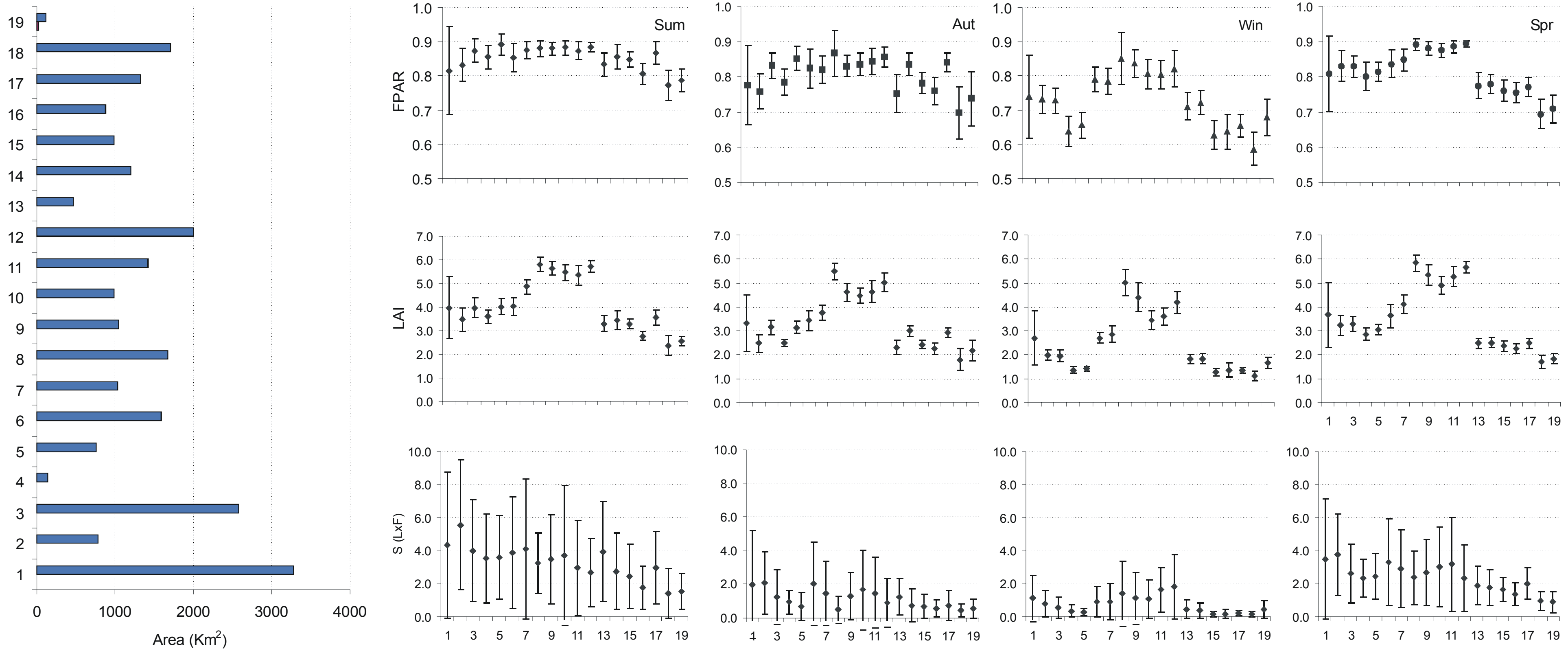

Figure 8. Area and seasonal descriptors (means ± SD) of the 19 LAI/FPAR-based Ecosystem Functional Types.

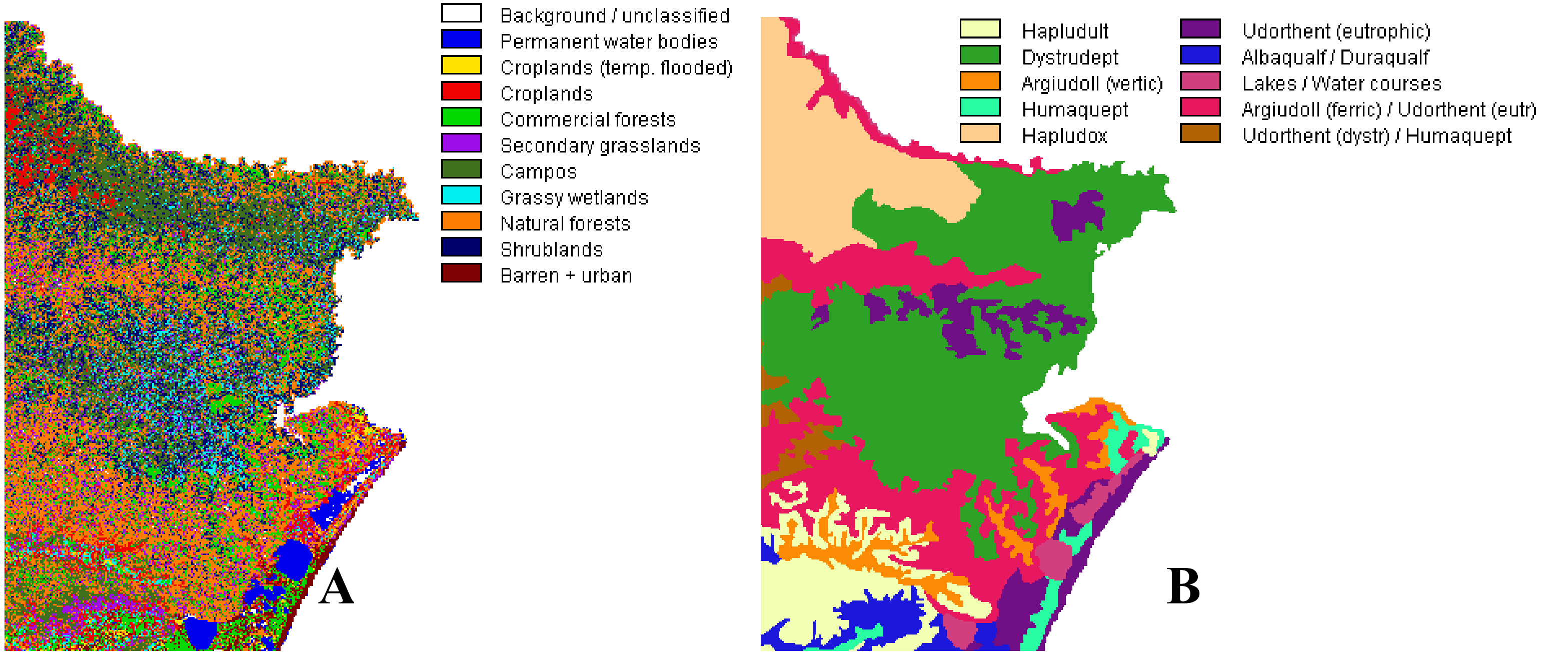

Figure 9. A- Main plant-cover types in the study area, as derived from Landsat bands 3, 4 and 5 and a digital terrain model. Pixel size of the Landsat bands: 0.01 km^2.

B- Regional soil units in the study area. After Streck *et al.* (2002). Classification equivalence between the Brazilian System of Soil Classification and the USDA Soil Taxonomy as provided by the '*Empresa Brasileira de Pesquisa Agropecuária*' (EMBRAPA) in the URL: http://www.cnps.embrapa.br/sibcs/

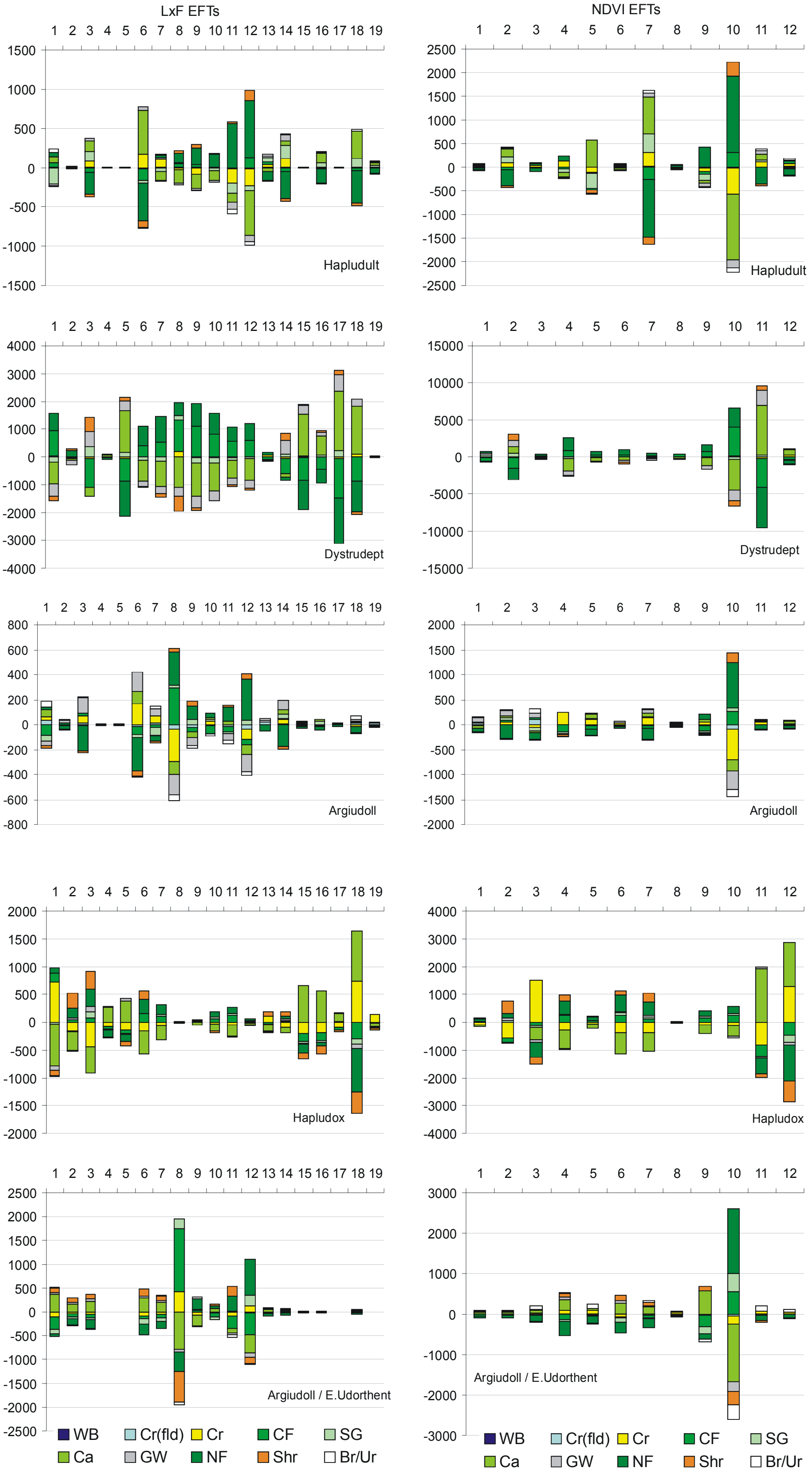

Figure 10. Land-cover type frequencies within the EFTs, presented as deviations from random expectation in each regional soil unit. Values in the Y axis: number of pixels above or below (-) the frequency expected for a random distribution of the LCTs within the EFTs. WB: Water bodies, Cr(fd): Croplands, temporally flooded, Cr: Croplands, CF: Commercial forests, SG: Secondary grasslands, Ca: Campos, GW: Grassy Wetlands, MF: Montane forests, Shr: Shrublands, Br/Ur: Barren / Urban.

APPENDIX.

A1. Two-dimensional contingency table of functional classifications. Joint frequencies given as shared number of pixels.

		NDVI EFTs												
		1	2	3	4	5	6	7	8	9	10	11	12	Total
LAI / FPAR EFTs	1	81	136	262	398	244	160	227	45	504	591	322	271	3241
	2	62	130	68	142	33	122	87	0	34	3	45	56	782
	3	514	692	113	230	56	254	239	1	24	0	421	33	2577
	4	13	23	9	0	0	2	0	0	0	0	51	49	147
	5	63	127	6	0	0	0	0	0	0	0	534	35	765
	6	16	85	64	300	252	119	414	3	211	61	52	13	1590
	7	59	38	47	280	96	137	107	3	184	61	18	9	1039
	8	0	3	38	13	9	1	3	51	10	1520	6	2	1656
	9	0	2	7	36	27	8	4	34	71	857	3	1	1050
	10	4	0	7	160	48	31	10	21	273	428	1	0	983
	11	0	1	21	85	94	6	16	30	293	866	4	1	1417
	12	0	2	12	24	14	1	4	49	126	1760	2	0	1994
	13	46	102	55	13	7	30	69	0	5	0	47	93	467
	14	162	279	54	52	37	48	165	0	1	0	353	48	1199
	15	72	178	31	0	0	2	5	0	0	0	579	123	990
	16	45	208	52	4	3	8	73	0	1	0	387	101	882
	17	138	227	16	0	0	3	6	0	0	0	871	61	1322
	18	44	191	197	0	4	5	74	0	1	0	777	418	1711
	19	2	11	19	0	3	0	19	1	0	0	46	22	123
Total		1321	2435	1078	1737	927	937	1522	238	1738	6147	4519	1336	23935

A2. Three-dimensional contingency table: Lai/Fpar- based functional classes in rows, land-cover types in columns and regional soil units in planes. Joint frequencies given as number of pixels. Land-cover types are: **NF** – Natural forest, **CF** – Commercial forest, **Ca** – *Campo*, natural grassland, **SG** – Secondary grassland, **GW** – Grassy wetland, **Shr** – Shrubland, **WB** – permanent water body, **Cr** – Cropland, with growing crop, **Cr(fld)** –cropland, temporally flooded, **Br/ur** – Tilled soil and urban.

Hapludult

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
1	0	21	750	677	648	1886	110	2340	127	106	6665	
2	0	0	16	4	5	26	4	18	0	2	75	
3	0	10	254	83	305	555	67	256	0	12	1542	
4	0	0	0	0	0	0	0	0	0	0	0	
5	0	0	0	0	0	0	0	0	0	0	0	
6	0	3	806	393	694	2014	152	1482	32	59	5635	
7	0	9	242	120	110	231	51	472	24	18	1277	
8	0	0	65	120	110	31	0	385	50	0	761	
9	0	0	45	137	131	109	0	592	64	0	1078	
10	0	0	134	101	125	195	9	586	38	8	1196	
11	0	0	369	451	478	1191	14	2221	114	1	4839	
12	0	0	238	502	455	539	0	2122	207	7	4070	
13	0	6	86	74	100	72	33	44	0	30	445	
14	0	14	301	119	387	530	102	250	0	35	1738	
15	0	0	0	0	0	0	0	0	0	1	1	
16	0	12	89	69	158	347	31	101	0	24	831	
17	0	0	4	2	4	9	0	1	0	0	20	
18	0	4	172	110	318	768	33	129	0	38	1572	
19	0	5	37	28	58	115	19	25	0	12	299	
F.jk	0	84	3608	2990	4086	8618	625	11024	656	353	32044	F..k

Dystrudept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	0	180	1996	648	3077	750	3278	2607	0	12536
2	0	0	42	255	179	917	172	890	745	0	3200
3	0	0	246	1303	2186	8259	3146	5724	6489	0	27353
4	0	0	11	12	41	256	73	85	165	0	643
5	0	0	40	58	834	4678	1301	868	2342	0	10121
6	0	0	88	981	346	1409	453	2171	1475	0	6923
7	0	0	87	1075	333	1476	474	2519	1516	0	7480
8	0	0	221	1485	412	152	66	1327	306	0	3969
9	0	0	40	1506	139	382	62	1881	999	0	5009
10	0	0	30	1269	138	624	140	1836	1045	0	5082
11	0	0	11	824	93	289	34	1007	579	0	2837
12	0	0	29	878	140	215	14	1272	632	0	3180
13	0	0	70	86	116	620	139	492	398	0	1921
14	0	0	91	499	918	3712	1658	2410	2900	0	12188

Dystrudept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
15	0	0	97	114	742	4910	1334	1196	2396	0	10789	
16	0	0	77	95	493	2684	747	850	1450	0	6396	
17	0	0	135	149	1406	7838	2291	2064	4015	0	17898	
18	0	0	220	142	785	5436	1370	1362	2479	0	11794	
19	0	0	17	20	6	85	38	54	78	0	298	
F.jk	0	0	1732	12747	9955	47019	14262	31286	32616	0	149617	F..k

Argiudoll

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
1	0	73	477	194	227	213	131	907	29	100	2351	
2	0	4	17	23	14	12	29	16	0	8	123	
3	0	30	219	126	98	56	190	136	1	30	886	
4	0	0	0	0	0	0	0	0	0	0	0	
5	0	0	0	0	0	0	0	0	0	0	0	
6	0	18	529	156	193	219	287	454	1	44	1901	
7	1	28	235	86	51	54	121	308	7	46	937	
8	0	0	194	569	294	50	3	1065	83	10	2268	
9	0	2	241	109	192	31	28	596	68	18	1285	
10	0	4	194	39	104	71	37	360	22	22	853	
11	0	0	211	91	104	98	22	533	39	2	1100	
12	0	0	331	201	289	71	9	1156	94	32	2183	
13	0	21	26	19	17	7	21	11	0	18	140	
14	1	15	172	90	112	85	122	87	0	18	702	
15	0	6	5	14	0	0	8	4	0	7	44	
16	0	3	25	8	44	24	15	33	0	1	153	
17	0	0	7	8	4	0	1	1	0	6	27	
18	3	13	21	30	15	16	26	16	0	30	170	
19	0	12	10	5	7	3	14	20	2	1	74	
F.jk	5	229	2914	1768	1765	1010	1064	5703	346	393	15197	F..k

Humaquept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	3	212	142	196	84	4	35	227	0	502	1405
2	0	22	6	35	2	0	8	7	0	43	123
3	0	39	23	36	4	0	15	45	0	85	247
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0
6	2	22	42	92	9	2	25	54	0	105	353
7	1	57	62	40	37	1	18	92	0	69	377
8	0	3	25	45	22	1	2	103	0	139	340
9	0	3	22	9	20	0	1	40	0	18	113
10	0	4	131	22	60	0	9	102	0	26	354
11	0	8	37	78	15	0	10	61	0	60	269
12	0	4	76	10	40	0	1	86	0	3	220

Humaquept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
13	0	12	11	18	2	0	5	12	0	24	84	
14	0	34	12	46	5	0	6	13	0	41	157	
15	0	9	6	8	1	0	3	11	0	7	45	
16	0	11	5	32	0	0	12	20	0	19	99	
17	0	0	0	0	0	0	0	0	0	0	0	
18	0	32	20	50	6	0	27	42	0	127	304	
19	0	4	6	5	3	0	9	14	0	29	70	
F.jk	6	476	626	722	310	8	186	929	0	1297	4560	F..k

Hapludox

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
1	0	0	1461	531	217	2643	265	1374	1636	0	8127	
2	0	0	389	315	162	2166	285	1132	1529	0	5978	
3	0	0	72	338	276	1906	336	1205	1514	0	5647	
4	0	0	66	21	30	944	83	130	330	0	1604	
5	0	0	22	9	42	1021	108	159	290	0	1651	
6	0	0	36	258	72	521	86	588	637	0	2198	
7	0	0	36	167	61	205	40	341	244	0	1094	
8	0	0	0	2	7	21	6	14	4	0	54	
9	0	0	7	20	13	13	2	42	26	0	123	
10	0	0	11	83	37	70	9	177	69	0	456	
11	0	0	11	159	46	74	4	210	141	0	645	
12	0	0	0	28	14	25	1	51	33	0	152	
13	0	0	453	151	89	1481	152	577	890	0	3793	
14	0	0	24	70	60	462	83	252	370	0	1321	
15	0	0	157	45	81	2345	166	463	753	0	4010	
16	0	0	272	83	117	2654	202	709	933	0	4970	
17	0	0	15	17	51	680	56	215	248	0	1282	
18	0	0	1510	93	145	4427	285	546	1429	0	8435	
19	0	0	178	7	2	98	11	38	45	0	379	
F.jk	0	0	4720	2397	1522	21756	2180	8223	11121	0	51919	F..k

Udorthent Eutrophic

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	27	48	226	617	428	511	116	1149	431	1056	4609
2	0	0	16	87	87	263	68	409	247	0	1177
3	0	4	37	157	210	747	235	843	514	10	2757
4	0	0	0	3	2	17	4	17	15	0	58
5	0	0	1	3	37	151	68	59	78	0	397
6	1	39	116	251	118	198	73	410	230	250	1686
7	1	0	28	179	85	211	56	525	206	14	1305
8	2	1	68	100	43	30	3	113	6	137	503
9	1	5	37	206	42	56	10	357	81	35	830
10	0	1	40	276	61	173	30	699	311	8	1599
11	0	3	17	124	45	60	13	321	139	11	733

Udorthent Eutrophic

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
12	0	1	33	106	34	20	1	135	64	37	431	
13	1	1	0	8	15	34	8	41	20	5	133	
14	0	20	58	114	140	282	95	344	126	189	1368	
15	0	0	6	12	71	322	72	141	141	0	765	
16	0	4	2	8	54	197	72	88	70	27	522	
17	0	0	13	17	111	821	220	272	341	0	1795	
18	0	17	12	102	169	565	142	237	227	364	1835	
19	1	7	10	44	23	0	6	31	4	48	174	
F.jk	34	151	720	2414	1775	4658	1292	6191	3251	2191	22677	F..k

Albaqualf

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
1	2	86	422	661	178	111	217	188	0	357	2222	
2	0	3	65	67	28	1	48	15	0	39	266	
3	0	55	146	141	136	23	113	108	0	60	782	
4	0	0	0	15	0	0	0	0	0	1	16	
5	0	1	0	12	0	0	0	1	0	2	16	
6	1	66	510	403	479	258	185	219	0	170	2291	
7	0	15	72	72	35	29	36	32	0	39	330	
8	0	2	7	22	1	1	1	9	0	8	51	
9	0	0	3	0	4	2	0	3	0	0	12	
10	0	0	13	5	6	6	7	16	0	4	57	
11	0	0	6	2	6	11	1	18	0	0	44	
12	0	2	2	3	7	7	4	2	0	4	31	
13	2	21	125	103	97	4	70	21	0	57	500	
14	0	29	238	226	217	38	112	90	0	126	1076	
15	0	1	1	13	0	0	1	0	0	1	17	
16	0	19	182	215	145	44	93	60	0	80	838	
17	0	0	1	0	1	0	1	1	0	0	4	
18	1	81	414	918	139	73	224	45	0	363	2258	
19	0	25	77	208	23	12	57	22	0	103	527	
F.jk	6	406	2284	3086	1502	620	1170	850	0	1414	11338	F..k

Lagoon shores

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	1	15	10	12	16	0	37	7	9	107
2	0	0	1	0	2	5	0	11	1	0	20
3	0	0	0	0	0	0	0	9	3	0	12
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0
6	0	0	0	3	10	0	0	18	0	0	31
7	0	0	3	0	3	1	0	10	0	0	17
8	0	0	12	2	2	0	2	1	0	1	20
9	0	0	0	0	6	0	0	5	0	0	11
10	0	0	7	2	4	2	0	8	0	0	23

Lagoon shores

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
11	0	0	0	0	1	0	0	2	0	0	3	
12	0	0	0	1	4	0	0	12	2	0	19	
13	0	0	0	0	0	0	0	2	0	0	2	
14	0	0	0	0	0	0	0	0	0	0	0	
15	0	0	0	0	0	0	0	0	0	0	0	
16	0	0	0	0	0	0	0	1	0	0	1	
17	0	0	0	0	0	0	0	0	0	0	0	
18	0	0	0	0	0	0	0	0	0	0	0	
19	0	0	0	0	0	0	0	0	0	0	0	
F.jk	0	1	38	18	44	24	2	116	13	10	266	F..k

Argiudoll / Eutr.Udorthent

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
1	3	9	506	1423	1319	1188	135	4946	1201	67	10797	
2	0	0	30	146	107	274	30	477	229	0	1293	
3	0	0	24	115	136	316	74	399	210	0	1274	
4	0	0	0	2	2	2	1	6	2	0	15	
5	0	0	0	0	1	2	1	0	4	0	8	
6	0	0	84	429	298	538	58	1206	464	24	3101	
7	3	3	112	365	291	420	60	1041	364	44	2703	
8	0	6	1460	4006	2521	591	119	7896	1182	31	17812	
9	1	2	355	1076	956	336	48	3574	742	77	7167	
10	0	3	258	644	539	432	45	2233	511	23	4688	
11	0	0	526	1384	1372	728	58	5206	1274	5	10553	
12	0	4	1290	2615	2768	1053	84	9963	1898	73	19748	
13	0	0	5	33	11	81	13	68	53	0	264	
14	0	6	15	27	18	49	7	27	29	19	197	
15	0	2	0	2	1	10	1	6	5	0	27	
16	0	0	0	0	5	8	0	12	1	0	26	
17	0	0	0	0	0	0	0	0	0	0	0	
18	0	0	0	18	3	32	1	28	16	23	121	
19	0	0	0	0	0	0	0	0	0	0	0	
F.jk	7	35	4665	12285	10348	6060	735	37088	8185	386	79794	F..k

Dyst.Udorthent / Humaquept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	0	52	107	104	125	2	490	132	0	1012
2	0	0	9	6	14	19	4	39	19	0	110
3	0	0	13	21	22	63	9	85	30	0	243
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	1	0	0	0	0	0	1
6	0	0	22	61	34	77	2	166	74	0	436
7	0	0	34	66	53	100	8	241	80	0	582
8	0	0	7	34	7	11	0	75	50	0	184
9	0	0	5	61	42	22	0	313	86	0	529

Dyst.Udorthent / Humaquept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
10	0	0	26	93	82	118	3	414	150	0	886	
11	0	0	32	129	103	82	7	495	144	0	992	
12	0	0	44	134	101	65	6	601	155	0	1106	
13	0	0	1	0	1	7	0	5	3	0	17	
14	0	0	0	0	1	3	0	0	4	0	8	
15	0	0	0	0	0	0	0	0	0	0	0	
16	0	0	0	0	0	0	0	0	0	0	0	
17	0	0	0	0	1	0	0	0	0	0	1	
18	0	0	0	0	0	0	0	0	0	0	0	
19	0	0	9	1	0	4	0	1	1	0	16	
F.jk	0	0	254	713	566	696	41	2925	928	0	6123	F..k

A3. Three-dimensional contingency table: NDVI- based functional classes in rows, land-cover types in columns and regional soil units in planes. Joint frequencies given as number of pixels. Land-cover types notation as in A2.

Hapludult

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	0	29	36	17	9	20	8	1	9	129
2	0	6	307	128	365	690	54	303	1	35	1889
3	0	3	125	89	92	187	27	171	6	28	728
4	0	0	338	138	151	393	36	700	17	6	1779
5	0	11	556	521	447	2052	102	1937	56	48	5730
6	0	0	52	32	21	41	22	131	1	4	304
7	0	33	1037	422	1337	2769	246	1274	14	120	7252
8	0	0	7	23	31	56	0	135	14	0	266
9	0	0	421	345	418	1040	8	1904	84	16	4236
10	0	0	441	1100	1001	948	0	4543	473	0	8506
11	0	12	276	139	233	563	90	179	0	57	1549
12	0	19	118	106	62	138	30	66	0	31	570
F.jk	0	84	3707	3079	4175	8886	635	11351	667	354	32938 F..k

Dystrudept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	0	124	801	1349	4964	1692	3694	3574	0	16198
2	0	0	206	626	2153	8670	3234	3771	6109	0	24769
3	0	0	154	403	274	1314	408	1077	885	0	4515
4	0	0	124	1941	683	2577	674	4564	2765	0	13328
5	0	0	19	514	119	568	201	1044	691	0	3156
6	0	0	91	703	399	1500	335	2022	1105	0	6155
7	0	0	59	504	196	1063	278	1227	889	0	4216
8	0	0	7	398	11	68	11	260	166	0	921
9	0	0	56	1229	257	890	147	2225	1282	0	6086
10	0	0	299	5313	825	1126	198	6266	2978	0	17005
11	0	0	373	346	3612	22514	6726	5227	11654	0	50452
12	0	0	271	50	229	2204	486	506	882	0	4628
F.jk	0	0	1783	12828	10107	47458	14390	31883	32980	0	151429 F..k

Argiudoll

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	1	50	129	90	55	4	124	152	0	44	649
2	0	11	253	163	172	105	179	115	1	34	1033
3	3	118	128	134	38	27	156	182	4	112	902
4	0	25	605	79	196	144	108	682	5	31	1875
5	0	0	362	82	162	177	114	353	5	30	1285
6	0	9	109	33	33	16	47	116	0	20	383
7	0	7	460	140	213	186	177	374	5	73	1635
8	0	0	24	18	39	8	0	110	5	16	220

Argiudoll

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
9	0	7	353	76	131	159	94	655	11	11	1497
10	0	0	528	926	737	168	13	2990	315	17	5694
11	0	10	146	69	61	30	46	78	0	24	464
12	1	7	72	50	27	70	35	56	0	12	330
F.jk	5	244	3169	1860	1864	1094	1093	5863	351	424	15967 F..k

Humaquept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	66	24	18	8	1	7	80	0	36	240
2	2	48	37	86	10	0	31	53	0	100	367
3	12	142	61	193	42	0	26	194	0	563	1233
4	0	46	241	97	132	0	15	246	0	135	912
5	0	35	176	155	84	0	46	206	0	193	895
6	0	45	27	66	28	0	5	124	0	87	382
7	1	74	104	296	56	5	33	106	0	287	962
8	0	6	23	21	18	0	1	58	0	18	145
9	0	35	45	8	24	0	10	37	0	18	177
10	0	0	53	16	41	1	0	122	0	2	235
11	2	59	53	199	13	2	24	77	0	193	622
12	1	24	23	121	13	0	11	52	0	158	403
F.jk	18	580	867	1276	469	9	209	1355	0	1790	6573 F..k

Hapludox

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	0	10	42	50	337	57	252	200	0	948
2	0	0	196	239	302	3247	404	1426	2057	0	7871
3	0	0	2040	191	98	2234	166	471	1029	0	6229
4	0	0	37	385	137	622	113	983	874	0	3151
5	0	0	4	95	38	142	26	243	185	0	733
6	0	0	47	456	221	1010	223	1304	1123	0	4384
7	0	0	47	342	166	1107	236	1082	1217	0	4197
8	0	0	2	14	7	5	0	21	11	0	60
9	0	0	16	205	90	156	35	361	259	0	1122
10	0	0	18	309	80	140	9	485	269	0	1310
11	0	0	225	117	262	6404	526	1077	2191	0	10802
12	0	0	2510	128	129	6833	437	735	1986	0	12758
F.jk	0	0	5152	2523	1580	22237	2232	8440	11401	0	53565 F..k

Udorthent Eutrophic

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	0	30	121	193	582	197	698	358	1	2180
2	0	17	27	103	90	331	92	318	182	86	1246
3	32	66	218	416	186	137	90	324	121	1060	2650
4	0	4	127	254	238	439	127	918	462	27	2596

Udorthent Eutrophic

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
5	1	34	257	232	104	100	50	344	92	217	1431
6	0	0	16	110	86	294	58	429	253	6	1252
7	7	32	189	250	87	80	42	235	72	335	1329
8	0	1	29	38	24	7	0	119	15	19	252
9	0	0	19	212	147	266	45	774	310	0	1773
10	1	1	50	686	105	238	18	1228	519	48	2894
11	15	110	355	519	713	1873	651	1066	764	824	6890
12	2	51	103	231	155	321	84	229	105	519	1800
F.jk	58	316	1420	3172	2128	4668	1454	6682	3253	3142	26293 F..k

Albaqualf

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	21	9	15	1	0	10	18	0	4	78
2	2	49	277	418	268	62	151	114	0	199	1540
3	2	62	158	568	46	16	105	33	0	262	1252
4	0	9	12	12	8	9	25	25	0	1	101
5	0	24	235	143	143	128	94	183	0	60	1010
6	0	3	7	8	3	7	6	11	0	5	50
7	0	112	999	773	912	293	461	308	0	367	4225
8	0	0	1	10	1	8	0	6	0	2	28
9	0	1	8	5	7	0	4	14	0	6	45
10	0	0	6	3	9	10	0	31	0	0	59
11	2	82	523	819	167	74	317	117	0	430	2531
12	4	102	286	701	82	59	150	84	0	306	1774
F.jk	10	465	2521	3475	1647	666	1323	944	0	1642	12693 F..k

Lagoon shores

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur	
	1	2	3	4	5	6	7	8	9	10	Fi.k
1	0	0	0	0	0	0	0	6	0	0	6
2	0	0	0	0	0	0	0	0	0	0	0
3	1	15	82	81	52	4	2	71	0	73	381
4	0	0	19	0	4	3	1	3	1	0	31
5	0	1	4	0	4	0	1	7	0	1	18
6	0	0	3	1	3	7	0	14	4	0	32
7	0	0	6	0	5	0	0	5	0	0	16
8	0	0	0	0	0	0	0	1	0	0	1
9	0	0	1	3	17	10	0	41	6	0	78
10	0	0	0	4	14	1	0	32	2	0	53
11	1	1	14	15	3	0	0	6	0	18	58
12	0	2	17	19	8	0	0	7	0	31	84
F.jk	2	19	146	123	110	25	4	193	13	123	758 F..k

Argiudoll / Eutr.Udorthent

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
1	0	9	11	19	38	79	27	118	45	6	352	
2	0	0	6	20	31	70	29	61	44	0	261	
3	7	5	88	211	131	150	33	431	104	99	1259	
4	0	8	306	404	412	528	86	1320	465	41	3570	
5	4	12	154	174	137	138	32	405	102	110	1268	
6	0	0	54	325	176	446	84	793	359	0	2237	
7	0	1	57	136	141	281	43	400	200	60	1319	
8	0	1	144	259	226	95	25	753	137	25	1665	
9	0	0	663	1437	1296	1420	98	5011	1271	1	11197	
10	0	0	3319	9408	7976	2948	316	28536	5598	42	58143	
11	4	6	97	61	32	13	8	63	3	128	415	
12	3	6	56	54	20	20	7	57	7	58	288	
F.jk	18	48	4955	12508	10616	6188	788	37948	8335	570	81974	F..k

Dyst.Udorthent / Humaquept

	WB	Cr(fld)	Cr	CF	SG	Ca	GW	NF	Shr	Br/Ur		
	1	2	3	4	5	6	7	8	9	10	Fi.k	
1	0	0	1	6	8	15	5	21	14	0	70	
2	0	0	6	5	9	38	8	23	26	0	115	
3	0	0	19	6	6	18	1	48	20	0	118	
4	0	0	45	98	93	157	9	371	148	0	921	
5	0	0	2	12	7	21	1	56	20	0	119	
6	0	0	12	22	15	29	1	86	29	0	194	
7	0	0	14	24	12	41	0	86	33	0	210	
8	0	0	0	5	5	5	0	29	4	0	48	
9	0	0	55	135	104	200	7	575	156	0	1232	
10	0	0	105	448	353	227	15	1931	540	0	3619	
11	0	0	23	7	8	30	0	42	19	0	129	
12	0	0	35	3	2	27	1	38	9	0	115	
F.jk	0	0	317	771	622	808	48	3306	1018	0	6890	F..k

THE EFFECT OF SPATIAL SCALE ON FUNCTIONAL HETEROGENEITY: A CASE STUDY FROM SOUTHERN BRAZIL

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RESUMO

A heterogeneidade funcional é um atributo indiscutível dos sistemas ecológicos. Neste artigo essa heterogeneidade descreve a distribução de unidades espaciais discretas com uma trajetória similar do NDVI em 2002. Essas unidades, ou tipos funcionais de ecossistemas (TFEs), localizaram-se no Sul do Brasil, na região transicional entre biomas úmidos subtropicais e temperados. Produzimos 8 mapas de TFEs para a zona, cada um com diferentes parâmetros de escala espacial (tamanho de pixel e área de cobertura), e comparamos os resultados em três janelas dentro da área maior. As diferenças foram descritas em termos da riqueza, diversidade e correspondência das classes funcionais com unidades de vegetação. Essa correspondência foi analisada dentro de unidades específicas de solo. A mudança nos parâmetros de escala-espacial determinaram em grande medida mudanças na diversidade, forma e arranjo dos objetos espaciais classificados como TFEs. Porém, como o efeito da escala espacial não é independente da configuração da paisagem, a resposta da classificação funcional às mudanças de tamanho de pixel e cobertura

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não foram homogêneas entre as janelas. Em termos gerais, os controles ecológicos relacionados com a vegetação tiveram um efeito maior sobre a diversidade e a riqueza dos TFEs, enquanto os controles relacionados com o solo tiveram maior importância na determinação do arranjo espacial das unidades funcionais.

Na janela com maior heterogeneidade ambiental e mais estreita associação na distribuição de solo e vegetação, maior resolução e cobertura menor resultaram num arranjo menos diverso de TFEs. Nas outras janelas, com uma configuração de solos menos diversa, a distribuição espacial da vegetação foi menos influenciada pela distribuição das unidades de solo. Sob essas circunstâncias, um aumento do refinamento da escala espacial de análise revelou um cenário mais rico de entidades funcionais. Concluímos que a estrutura quantitativa (diversidade e riqueza) e o arranjo espacial dos TFEs responde à estrutura de grupos dentro dos datasets de NDVI. No entanto, semelhante estrutura responde à escala espacial de uma maneira complexa, através da heterogeneidade ambiental e vegetacional que é amplificada ou restringida ao se fazer *down-* ou *up-scaling*. Para uma visão detalhada da heterogeneidade funcional numa região, parece então apropriado não só empregar dados de maior resolução e menor extensão espacial, mas também modificar a sua cobertura de maneira a diminuir a heterogeneidade funcional compreendida. Isto é assim porque num cenário de menor diversidade ambiental, a classificação funcional dá maior importância à estrutura de grupos determinada pela distribuição em mosaico dos controles funcionais na vegetação.

Palavras chave: Heterogeneidade funcional, tipos funcionais de ecossistemas, MODIS NDVI, interação, associação espacial, unidades regionais de solo, tipos de cobertura da terra, configuração da paisagem.

ABSTRACT

Functional heterogeneity is an attribute of the ecological systems. In this paper, heterogeneity is identified with the distribution of discrete groups of pixels that share a similar seasonal trajectory of MODIS NDVI during the annual cycle of 2002.

The groups so defined are called ecosystem functional types (EFTs). The study is located in a transitional region between humid subtropical and humid temperate biomes in Southern Brazil. We produced 8 maps of EFTs, each map with different spatial-scale parameters (pixel-size and areal coverage), and compared them over three window sizes within the study area. Differences were described as richness, diversity and correspondence of the EFTs in shared pixels with vegetation units. The correspondence was assessed within specific environmental (soil) domains. We found that spatial-scale parameters emphasized the richness, shape and arrangement of the EFTs considered as spatial objects. Since the effect of spatial-scale is not independent of landscape configuration, the response of the functional classifications to changing pixel-size and coverage was dissimilar among the windows. In general terms, ecological drivers related to the vegetation had the greater effect on the richness and diversity of the EFTs, while soil-related drivers had a major role in determining the EFTs spatial arrangement.

In the window with greatest environmental heterogeneity and tightest soil – vegetation coupling, increasing resolution and smaller areal coverage was associated to a less diverse array of EFTs. The remaining windows have less diverse soil configurations and the spatial distribution of vegetation units is determined to a lesser extent by the soil units. Under those circumstances, a greater refinement of the spatial scale of the analysis revealed a richer scenario of functional entities. We conclude that the quantitative structure and spatial arrangement of the EFTs respond to the group-structure within the NDVI datasets, but that such a structure responds to the spatial scale in a complex manner, via the environmental and vegetational heterogeneity that is gained or lost when down- or up-scaling. If we seek a detailed picture of the functional heterogeneity in a given region, it seems appropriate not only to rely on high-resolution and/or spatially-constrained data but also to modify spatial-coverage in order to reduce environmental heterogeneity. This is so because in a scenario of restrained environmental diversity, the functional

classification gives more importance to the group-structure determined by the patchy distribution of vegetational drivers.

Key words: Functional heterogeneity, ecosystem functional types, MODIS NDVI, interaction, spatial association, regional soil units, land-cover types, landscape configuration.

Running title: Spatial scale and functional heterogeneity.

INTRODUCTION

Functional heterogeneity is an indisputably attribute of the ecological systems. It manifests itself, in time and space, over a very broad range of geographical scales and temporal domains. This notwithstanding, it has been largely ignored, with minimum detriment whenever its grain size was either much smaller or much larger than the extent of the study area or the spatio-temporal domain of the phenomenon under analysis. Notwithstanding previous practice, for the regional to global scales at which processes of environmental change are more evident, functional heterogeneity has to be addressed explicitly. According to Strayer (2005), functional consequences of heterogeneity can feed back onto the structure and function of the ecological systems, producing so a positive loop from which patterns of heterogeneity change in complex way. Functional heterogeneity in fact is as much a compelling driver of the ecosystem's response as it is a manifestation of the response it-self.

Functional heterogeneity emerges from the interaction between the abiotic template (which includes climate, topography and substrate), the biotic assemblages, the disturbance regime and human activities (Turner & Chapin 2005). It may be depicted as a discrete attribute, in terms of a patchy structure of functional entities, or as a continuous trait, in terms of some process-defined density gradient. Moreover, the characterization of functional heterogeneity largely depends on the function and parameters chosen, as well as on the spatial and temporal scales of interest (Franklin 2005).

In a previous work (Pinillos *et al.* in Chapter 3 this thesis) we discussed the effect of functional parameters, and hence the effect of function on the resulting map of heterogeneity. Functional heterogeneity accounted for the distribution of the discrete units enclosing areas with a similar seasonal trajectory of MODIS parameters (LAI, FPAR and NDVI) during the annual cycle of 2002. These units, the ecosystem functional types (EFTs, after Paruelo *et al.* 2001), were located in a transitional region between humid subtropical and humid temperate biomes in Southern Brazil. Parameters were sorted in a way that one functional classification responded to the intra and inter-seasonal variation of the reciprocal effect of LAI and FPAR, while the second to the seasonal progression of the NDVI and its within-season range of variation. We observed that the two functional maps differed in terms of richness and spatial configuration of their categories, proving so that functional heterogeneity is heavily dependent on the variables chosen to describe ecosystem functioning. Likewise, differences were also evident in terms of the patterns of interaction of the functional maps with: 1- a land-cover classification based on vegetation physiognomy and land-use, and 2- the regional distribution of soil classes. This observation has established the fact that different maps of functional heterogeneity also diverge in terms of their sensitiveness to similar vegetational and environmental drivers.

In the present paper we proceed with the analysis of the factors influential on the recognition of functional heterogeneity by examining the effect of the spatial scale. For remote sensing imagery, spatial scale is defined after King (2005) as the physical characterization of the spatial dimension of the study area. This takes the form of two measurement parameters, areal extent and pixel size. An additional parameter, location, indicates the geographic domain of the dataset. Location and extent constitute the dataset areal coverage. All these parameters have been referred to by Jelinski and Wu (1996) as the basis of the Modifiable Areal Unit Problem (MAUP). The MAUP establishes that the modification of areal coverage and/or pixel size will likely modify the results of spatial pattern analysis on a set of aggregated data and therefore will challenge the inferences so-derived. These parameters, however, would be variably influential. Turner *et al.* (1989) showed that their effect depends on how spatial pattern is described and on the inherent properties of the region under analysis. As such, it is essential for understanding how ecological patterns and processes relate to one another in the space to assess the variation of landscape attributes (for example, the richness and arrangement of functional categories) in relation to different spatial scales.

The purpose of this study is to do exactly that. Taking as a study case a forest-to-grassland transitional region in Southern Brazil, we observed the effect of changing spatial-scale parameters on the classification of ecosystem functional types. We further examined how changes produced by scaling affected the inferred relationship between the functional categories, the vegetation and the environment. As in our previous work (Pinillos *et al.* in Chapter 3, this thesis), the vegetation is portrayed in terms of a land-cover classification based on physiognomy and land-use, while main environmental (biotic, geomorphic, climatic and lithological) factors are represented by the regional distribution of soil types.

THE STUDY AREA

The characteristic vegetation of the passage from the biome of *Mata Atlântica* to the *Pampa* prairies of southern South America is a mosaic of grasslands (*campos*) and forests. This mosaic dominates the landscape over the plateaux of the Brazilian states of Paraná, Santa Catarina and Rio Grande do Sul (Hueck 1972, Klein 1975, Alves-Alonso 1977). Farther to the north, from São Paulo State down to Paraná State, the landscape is marked by a dominant forest physiognomy, where tropical evergreen formations gradually give place to subtropical semideciduous forests. Farther to the south (in the meridional half of Rio Grande do Sul and the Pampas region of Uruguay and central Argentina) there is a definite dominance of physiognomies characteristic of the temperate prairies. Since both types of physiognomies, as well as many of their more conspicuous floristic elements, are present over the area spanning from about 25° to 30° S, in the mosaic-like landscapes of the south Brazilian plateaux, the whole region is considered a wide subtropical ecotone between the humid biomes of subtropical forests and temperate grasslands.

The subtropical belt, with average thermal amplitude (mean temperature difference between the coldest and warmest months) of 8° to 10°C, has in fact transitional characteristics between the constant monthly temperatures that characterize tropical climates, and the fairly contrasted seasonal regime of the warm temperate zone. As there is a significant altitudinal gradient of about 1000 m asl., the mean annual temperatures range from 20o to 14°C. Likewise the mean number of frost days increases accordingly from 1 per year, in the coastal plain, to more than 30 days on the summits (Nimer 1989). The whole region has a humid climate, with a slight eastward (seaward) precipitation gradient from above 1800 to ca. 2300 mm yr.

The study area (Figure 1) is located in the northeastern corner of Rio Grande do Sul, extending from latitude 30° S to 28 °S, and from longitude 51 °W to 49.5 °W. Greater products of tectonics and geomorphic dynamics are recognizable by the division of the area into four major types of landscapes: 1- The Quaternary coastal plain, 2- the central depression, 3- the *Serra Geral* and 4- the tablelands on the plateau. In each landscape unit, distinctive patterns of soil, land-use and vegetation distribution are readily recognized. Mosaics of natural (mixed montane and semideciduous) forests dominate over the older and more dystrophic soil units in the central depression and the higher tablelands. These mosaics have been replaced to a variable degree by commercial forests and pastures, and only secondarily by agricultural fields. Croplands abound on the young depositional soils of the coastal plain, while on the also young yet erosional soils of the *Serra Geral* natural forests intermingle with isolated patches of *campos*, agriculture and forestry. For each major landscape unit the frequency of soil types and land uses, as they were established according to remote imagery from the second semester of 2001, appear in Table 1. A more detailed description of the study area is found in Pinillos *et al.* (Chapter 3, this thesis).

METHODS

Ecosystem functional type classification

Ecosystem functional types were identified on the basis of MOD13 imagery (MODIS NDVI) whose pixel size varies from 0.0625 to 1 km^2. The period considered for analysis comprehends from 16-Dec 2001 to 31-Dec 2002. MODIS images were cropped to fit the study area and reprojected to conform to the World Geodetic System 84 (WGS84). Time-series of NDVI were grouped into seasons, images with abnormally low records were excluded, and descriptors were calculated for each pixel in a per-season basis. We based the functional classification on the trajectories through the year 2002 of three descriptors: mean seasonal NDVI, maximum seasonal NDVI and minimum seasonal NDVI.

Descriptors in a season were used to produce a seasonal classification (map of seasonal types or STs) by means of a CLUSTER routine. CLUSTER is a simple histogram-peak technique of classification equivalent to looking for the peaks in a *n*-dimensional histogram (as many dimensions as number of bands or descriptors used), where a peak is defined as a value with a greater frequency than its neighbors on either side. Once the peaks have been identified, all possible values are assigned to the nearest peak and the divisions between classes fall at the midpoints (Eastman 2006). Thereafter, the overlaying of consecutive seasonal maps allows the recognition of groups of pixels with similar ST sequences. When these groups occupied at least one percent of the study area, they were deemed relevant to our study. We used these to set the number of EFTs and to develop signature files for EFT classification. Pixels belonging to the discarded groups were reassigned to the other groups by a Maximum Likelihood classification routine (Richards, 1986). A detailed account of the procedure is found in Pinillos *et al.* (Chapter 3, this thesis).

Scale effect and functional classifications

Based on the sequential method described earlier, we constructed maps of ecosystem functional types from MOD13 imagery with eight different sets of spatial-scale parameters. Spatial scale was defined by the parameters shown in Table 2. Spatial coverage parameters defined four windows, one for total study-area coverage (T) and three more for smaller areas within the first (W1, W2 and W3, Figure 2). For each window, we performed functional classifications at two different pixel-sizes: 0.0625 and 1Km^2 (pixel side 250m and 1Km, respectively), producing eight functional classifications: T-1Km, T-250m, three W*n*-1Km and three W*n*-250m (n = 1, 2, 3). To make the comparisons feasible between classifications of differing coverage, maps T-1Km and T-250m were cropped to fit the sub-areas W1, W2 and W3, giving rise to thee maps Tw$_n$-1Km and to a similar number of Tw$_n$-250m maps.

We consider the maps available for Window 1: Tw1-1km, Tw1-250m, W1-1km and W1-250m. Dissimilarities between Tw1-1km and Tw1-250m are the outcome of different pixel sizes, as well as dissimilarities between W1-1Km and W1-250m. Conversely, dissimilarities between TW1-1km and W1-1km result from the differing spatial coverage of the source data, while dissimilarities between TW1-1km and W1-250m reflect differences in both spatial coverage and pixel size. Differences among classifications were firstly presented in terms of their structural attributes: richness and diversity. Richness (S) is defined as the numerousness of the categories in the classifications. Diversity (H), in turn, refers to the entropy of their structure, given as the frequency distribution of individual pixels in the classes (see Orlóci 1991, Orlóci 2006, and Orlóci *et al.* 2002). The diversity of each classification, H, was measured as a Renyi's entropy of order one, equivalent to Shannon's entropy $H = -\sum_{i=1}^{c} p_i \ln p_i$ (Eq. 1), in which c is the number of functional categories and p_i is the relative frequency the *i*th category.

We also performed pair-wise comparisons between the maps of any given window. Taking *ff* and *gg* as one possible pair of maps in Window 1, *ff* and *gg* were contrasted in terms of a normalized information metric $d_{fg} = 1 - \frac{I_{ff} + I_{gg} - I_{f+g}}{INF(I_{ff}, I_{gg})}$ (Eq. 2), which is the one complement of the information shared by the two maps, expressed in units of the theoretical maximum of mutual information, which happens to be the lesser *(INF)* of I_{ff} and I_{gg}. Among the symbols I_{ff}, I_{gg} and I_{f+g} represent the information in map *ff*, in map *gg* and jointly in the maps *ff* and *gg*. The difference $I_{ff} + I_{gg} - I_{f+g}$ is the term that represents *ff* and *gg* mutual information (or interaction), I_{fg}. The metric d_{fg} itself range in value between 0 (complete identity of the two maps) and 1 (maximum difference). An exact $d_{fg} = 1$ is unattainable in real data. Similar comparisons were made for the EFT maps in windows 2 and 3. It was assumed that the greater the dissimilarity, the stronger the influence of the spatial scale parameters on the functional classifications.

The complement $1 - d_{fg}$ is analogue of the coherence coefficient,

$$r_{fg} = \frac{I_{ff} + I_{gg} - I_{f+g}}{I_{f+g}} \qquad \text{(Eq. 3),}$$

which is interpretable as a similarity measure on the scale of 0 and 1 with 0 indicating maximum dissimilarity and 1 maximum similarity. In this case 0 would be practically unattainable. The coherence coefficient r_{fg} can also be presented in the form $C_{fg} = \sqrt{r_{fg}}$ (Eq. 4), which approaches unity as the interaction between *ff* and *gg* increases in relation to their joint information.

By means of the coherence coefficient in Equation 4 (C_{fg}) the four functional classifications per window where contrasted with the corresponding areas of: 1- the Map of Regional Soil Units of Rio Grande do Sul (Streck *et al.* 2002) and 2- a land-cover classification on Landsat bands dated from August to November of 2001. The map of regional soil units has an original resolution of 1:750,000 and covers the entire state of Rio Grande do Sul. As such, it was cropped to fit the study area and resampled to the pixel size of the land-cover classification classification. In turn, the land-cover classification was derived from Landsat bands resampled to a pixel size of 0.0081 km^2 and reprojected to conform the Lat/Lon WGS84 system. For further information on the land-cover classification procedure see Pinillos et al. (Chapter 3, this thesis). In order to make comparisons feasible, the EFT maps were also resampled to the pixel size of the land-cover classification. Comparisons allowed measuring to what extent the change of spatial scale affects the association of the functional classifications with the regional types of vegetation and soil. Further details on the rationale of the information-based indices in equations 1 to 4 can be found in Orlóci (1978, 1991, 2006).

As seen, both metrics, the Coherence Coefficient and the Normalized Diverge Coefficient, rely on the interaction term I_{fg}, which has to be statistically significant in order to produce equally significant metrics. To determine the probability of having an interaction term as high as the observed, we used random pixel samples and tested for sampling sufficiency (Pillar 1998). The I_{fg} values were calculated for the samples and tested for significance in randomization experiments under the null scenario of a random distribution of the categories of one classification over the categories of the other. Typical to our case, the labels of one classification were randomly permuted among pixels while keeping unchanged pixel's identities for the other classification. This is the default procedure in MULTIV, the software used for the purpose (Pillar 2004), which is available at http://ecoqua.ecologia.ufrgs.br. We used this package to perform 10,000 randomization steps. After each, the contingency table and the I_{fg} values of each paired comparison were recomputed. We estimate the probability of an at least as extreme I_{fg} value occurring by chance as the observed, $P(I_{fg\ (\text{rand})} \geq I_{fg})$, by the proportion of randomization-steps scoring values equal to or higher than the observed I_{fg}. If $P(I_{fg\ (\text{rand})} \geq I_{fg}) <= 0.05$, the information term is deemed statistically significant at a confidence interval of 0.95.

In our previous studies we observed that not any EFT corresponded to a single land-cover type (or LCT), since the composition of the functional classes, in terms of LCTs, largely depended on functional convergences among the land-covers. However, there was also a variable degree of randomness due to errors in the source data and to the different spatial resolutions at which the functional and the LCT classifications were performed. In the same way, we established that the ambiguity in the relationship among LCTs and EFTs diminished when their joint frequencies were analyzed in a constrained environmental space, such as the domain of regional types of soil. Here we assess the influence of spatial-scale parameters on the association of the EFTs and LCTs in the different soil units. To do this analytically, we produced a three-dimensional contingency table for each EFT map. Sorting criteria of the rows (*i*) was the functional classification, with categories $i = 1, \ldots, h$. Sorting criteria of the columns (*j*) was the land-cover classification, with categories $j = 1, \ldots, w$. And the sorting criteria of the planes (*k*) was the soil taxonomy, with categories $k = 1, \ldots, d$.

In each *k*th category of the soil taxonomy, we calculated the deviation from random expectation for the *j*th land-cover in the *i*th EFT as $D_{ij|k} = X_{ij|k} - Y_{ij|k}$ (Eq. 5). $X_{ij|k}$ is the joint frequency of the *i*th EFT and the *j*th LCT, and $Y_{ij|k}$ is the expected joint frequency under the null scenario of no association between the two sorting factors. $Y_{ij|k} = \dfrac{X_{\cdot jk} X_{i \cdot k}}{X_{\cdot\cdot k}}$ (Eq. 6) in which $X_{\cdot jk}$ is the sum of the *h* frequencies in the *j*th column of the *k*th plane, $X_{i\cdot k}$ is the sum of the *w* frequencies in the *i*th row of the *k*th plane and $X_{\cdot\cdot k}$ is the overall sum of the $h \times w$ frequencies in the *k*th plane.

Some of the deviations would be positive (frequencies higher than random expectation) and some others would be negative, indicating mutual inclusion or exclusion respectively. We summed up positive deviations ($D_{ij|k} > 0$) in the rows, finding so the overall positive deviation associated with each EFT in each *k*th soil unit ($+\Delta_{ik}$). Likewise we summed up negative deviations ($D_{ij|k} < 0$) to find $-\Delta_{ik}$. We also identified maximum positive and negative $D_{ij|k}$ in each *i*th row ($_{\max}{+}Dij_{|k}$ and $_{\max}{-}Dij_{|k}$). When a given $_{\max}(\pm)D_{ij|k}$ was at least 50 percent of $+\Delta_{ik}$ or $-\Delta_{ik}$, we concluded that *j*th land-cover have a clear association, either positive or negative, with the *i*th EFT in the *k*th soil unit. We then compared the four functional classifications in a given window, in terms of the number of clear LCTs / EFT associations it produced.

It should be mentioned further that by contrasting the results of all the analyses performed on maps of different windows yet with similar spatial-scale parameters, we obtain a variation that should be explained in terms of local factors, such as the spatial arrangement of landscape components or landscape grain size. For this we characterized the landscape in each window by means of: 1- the richness and diversity of environmental (soil) units (S_E and H_E), 2- the richness and diversity of vegetational (land-cover) units (S_V and H_V), and 3- the degree of fragmentation of the landscape. Richness was defined the same way as for the functional classifications, the number of environmental or vegetational classes in the area, while diversity was measured by Renyi's entropy of order one (Equation 1).

Landscape fragmentation was expressed by a Fragmentation Index (F_n) calculated on the land-cover classifications. Defined after Monmonier (1974), it was computed for running kernels of 7 x 7 pixels in a simple manner: $F_n = \frac{n-1}{c-1}$ (Eq. 7), in which n is the number of classes in the kernel and c the number of pixels considered. We calculated the average Fragmentation Index for each window (F_n) and for the soil classes occurring inside ($F_{n|k}$). Equally important to understand the alterations of functional heterogeneity with changing spatial-scale, is to appraise how the domain of variability of the functional descriptors (seasonal mean, minimum and maximum NDVI) is enlarged or reduced when areal coverage and/or pixel size varies along the scaling ruler. As such, we computed for the total area and the three windows, at the two pixel-size, the average values and their associated relative variation coefficients, of the 12 seasonal descriptors of the NDVI.

RESULTS

In Figure 3 we present the resulting maps of EFTs in the three windows. Associated values of richness (*S*) and Diversity (*H*) appear in Table 3. Our results suggest that the spatial coverage of primary data plays a foremost role to define EFT richness and diversity, on account of the richer and more diverse classifications provided by spatially-restricted datasets in windows 1 and 2. Likewise, highest richness and diversity were attained in Window 2, which had the lesser spatial extent. Nevertheless, classifications in Window 3 showed the opposite pattern, with the richest and more diverse classification resulting from the dataset with the lesser spatial-scale refinement. These observations imply that local factors greatly influence the relationship between spatial coverage and the variety and diversity of functional entities. There are no consistent trends linking richness and/or diversity with pixel-size.

Divergences among functional classifications are presented in Table 4. Larger divergences per window always involved maps of differing pixel size, which suggest a greater influence of that scale parameter on the interaction between functional classifications. Nonetheless, maps based on window-specific data deviated more from each other, with changing pixel size, than the maps obtained for the totality of the study area. In window 3, for instance, the conjunction of both scale parameters rendered the highest divergence. This observation implies a synergetic effect of pixel size and spatial coverage on shaping and delimiting functionally-homogeneous areas in a given region.

Regarding the paired comparisons between functional entities, land-cover types and soils by means of the Coherence Coefficient, C_{fg} (Table 5), we found in every case higher coherences between EFT and soil maps than between EFT and land-cover maps. We also observe an overall trend of increasing coherence between EFT and soil maps at the coarse resolution of 1 km^2. These results point up the influence of the consistency of spatial scale of the classifications being compared on the coefficient. A scale of lesser detail helps the functional map to enhance mutuality with the soil classification, which was obtained at the state level and at a proximate scale of 1: 750,000 (proximate pixel size: 1 km^2). Regarding the effect of spatial scale upon the coherence between the EFT and LCT maps, it seems to be window-specific. In the first window functional maps at the middle of the scaling ladder (T_{W1}-250m, W1-1Km) attained the highest coherences with the land-cover classification. In the second window, the index had the lesser variation along the scaling ruler, yet functional classifications at extreme positions (T_{W2}-1Km, W2-250m) display the largest coherences with the LCT map. In the third window, coherences show a clear and important improvement with increasing pixel-size. Worthy of attention are the notable differences among windows of the LCTs / soil units coherences, which reflect sensible divergences of the three sub-areas in terms of the spatial arrangement of their landscape components. These landscape differences among windows are plausible causes of the non-uniform behaviour of the EFT/LCT coefficients along the scaling ruler.

All the interaction terms, I_{fg}, associated with the Normalized Divergence and Coherence Indices were numerically robust and quite improbable under the null scenario ($P(I_{fg\ (\mathrm{rand})} \geq I_{fg}) << 0.05$). As such, we infer the statistical significance of the derived metrics, C_{fg} and d_{fg}.

In the Appendix we present the three-dimensional contingency tables with the joint frequencies of functional entities, LCTs and soil units (Table A1). Maximum positive and maximum negative deviations from random distribution (${}_{\max}(\pm)D_{ij|k}$), associated with the land-cover types in each EFT and soil unit also appear in the appendix (Table A2). These deviations are presented there as ratios of the total negative and positive deviations associated to the corresponding EFTs in the soil unit (i.e. ${}_{\max}{}^{+}D_{ij|k}\ /{+\Delta_{ik}}$ and ${}_{\max}{}^{-}D_{ij|k}/{-\Delta_{ik}}$). These ratios, when higher than 0.5, identify those cases in which we conventionally assumed a given EFT to be clearly associated either with the presence (positive deviations) or with the absence (negative deviations) of specific LCTs in a particular soil unit. That is to say that such an EFT is a strong predictor either for the presence or the absence of a given land cover. In Table 6 we present, for the 12 functional classifications, the number of land-cover types having ${}_{\max}{}^{(\pm)}D_{ij|k}\ /{(\pm)\Delta_{ik}} > 0.5$ in each ith EFT and kth soil unit. Taking the values as proportions of the total number of functional entities occurring in the soil unit, we obtain the relative number of EFT/LCT matches for a given classification in the kth soil unit. We do not observe any general trend that relates these relative numbers with the spatial-scale parameters of the corresponding functional maps. Neither have we found such a pattern when we analyze each window independently. However, what we do observe is that the ratio of EFT/LCT matches in a given window varies more between soil units than between functional classifications at different spatial scale. Taking as an example Window 1, in the domains of the *Dystrudepts*, *Hapludox* and *Udorthents*, both positive and negative associations increase with increasing scale refinement. In the remaining soil domains the relationship is uncertain. Therefore we conclude from the deviations that, similarly to what we have concluded from the analysis of coherence coefficients, the relationship between land-cover and functional entities seems largely dependent on landscape characteristics specific to each window, and only secondarily on the spatial-scale parameters of the functional datasets.

Regarding landscape traits in the windows, in Table 7 we define the areas in terms of the richness and diversity of their landscape components. Notice similar patterns of richness, yet quite contrasting patterns of LCT and soil diversity among windows. In the three areas, soil richness and diversity are directly related, in a way that Window 2 has the smallest values of the two descriptors and Window 3 the largest. However, LCT richness and diversity behave in a different fashion, with the first and second windows having the lesser richness, yet the highest diversity, and Windows 3 having highest richness but lowest diversity. Conversely, LCTs fragmentation does not seem to differ among the windows (Table 8). The index roughly converges on 0.28, indicating a relatively homogeneous, moderate degree of LCT fragmentation in the study area. Neither the fragmentation indices show remarkable differences between soil units within a given window nor between soil units occurring in different windows. This notwithstanding, standard deviations in relation to the mean reveal that within windows and within soil units the fragmentation index may drift from the mean up to 50 percent. This reveals a moderate variability of the size and arrangement of the land-cover units that remains unexplained either by differences among windows and soil classes.

The functional variability comprised by the NDVI data sets varied to a large degree among sub-areas. In Figure 4 we present the relative-variation coefficients associated with each seasonal descriptor of the NDVI, as these changed from the fine to the coarse pixel-size, and from total to each window-specific coverage. First thing to be noticed is the slight increase of variability that comes with increased data resolution, in a way that relative variation coefficients tend to be higher in the datasets with 0.0625 Km^2 pixel-size. It is also noticeable that cropping the datasets to fit spatially-restricted windows in some cases enhanced the coefficients, as it was the case in the third and first windows, and for most of the NDVI descriptors in summer, autumn and spring. It worked differently in the second window, for which restricted areal coverage diminished the variability of the functional descriptors. The exception of this behavior occurred in winter, when relative variation coefficients in Window 2 attained the highest values.

DISCUSSION AND FINAL REMARKS

Spatial scale parameters determined, largely, the richness, shape and arrangement of the spatial objects identified by the EFT classification. We have framed our subject in what has been called in the literature the Modifiable Areal Unit Problem (MAUP: see Jelinski & Wu 1996, and references therein). The MAUP refers to the potential variation of the results of spatial-analyses coming from altering the definition of the units from which data is collected. This problem is particularly important when we deal with multi-scale spatial phenomena. According to the aforementioned authors, the MAUP applies to two separate yet interconnected problems: the scale problem, in which the same data is aggregated into sets of larger areal units (pixels), and the zoning problem, in which the same set of areal units is recombined into zones that are of the same size but located differently.

The zoning problem is not handled in this paper, since we did not survey the effect on the functional classification of having similar sized windows with different degree of overlapping. This could have resulted in somehow differently located pixels within the overlapped area and possibly in a different configuration of the functional units inside. However, that problem was not of our concern in this paper. Yet, we enlarged the scale problem by adding to the effect of the size of the areal unit the extent and coverage of the study area. While pixel-size and spatial extent change the size of the spatial dataset from which to derive patterns of functional heterogeneity, by including locational differences among windows (differing spatial coverage), we also include the influence of dissimilar landscape configurations. Results so far obtained have been consistent at showing that the effect of spatial-scale is not independent of landscape configuration.

In general terms, by changing any of the defining parameters of spatial scale we obtain different pictures of functional heterogeneity. When we compared the functional heterogeneity depicted at different spatial-scales, we observe important changes regarding richness and diversity. These are traits describing the structure of the functional classifications, which appear to be more responsive to variations on the spatial extent than to changing pixel-size. In an apparently contradictory way, paired comparisons of the classifications by means of the divergence coefficient show a greatest departure of one classification to the other with changing pixel-size. At this point it is relevant to clarify the meaning of the divergence coefficient, which measures, in relative terms, how much a pair of maps fails to attain their maximum possible mutuality. This mutuality refers to the extent to which the frequency distribution of the states in the first map comes close in probability terms to the states in the second map. The larger this probability, the more any functional category in one map is predicted by one or several categories in the second map. As such, though varying spatial-extent has the largest influence on the structural traits of the functional classifications, is pixel-size the parameter with greatest effect on their interdependence.

Being functional heterogeneity an emerging property of the vegetation in relation to its environment, it follows that the spatial arrangement of vegetational and environmental traits must be somehow mirrored by functional heterogeneity. This should be so provided that these traits are meaningful drivers of the function for which heterogeneity is described. The fact that coherence interactions in Table 6 are all highly significant points in that direction. However, meaningful drivers of ecosystem functioning usually express themselves at different spatial scales, in a way that makes necessary a multi-scale approach to functional heterogeneity and patchiness (see for instance, Kotliar & Weins 1990, Wu & Loucks 1995, and references therein). Our results indicate that when we change the spatial-scale at which functional patchiness is portrayed, we may enhance or reduce the mutuality between the map of functional entities and its vegetational or environmental counterparts. This is certainly so because, *given the different spatial-scale parameters at which the soil and land-cover maps were obtained, the drivers whose spatial distribution is described in each one of these maps operate upon functional heterogeneity at different domains of the scale*. Differences between windows, in turn, express the changing spatial domain of the vegetational and environmental traits considered, changes that are manifested in the variation of mutuality between soil and land-cover units when moving from one window to next (Table 5).

When we compare the structural traits of the functional classifications in each window, with the structural traits of the corresponding land-cover and soil maps, the maximum EFT richness and diversity is attained in the window for which maximum diversity of land-cover classes was found (W2 - 250m). The second largest functional richness and diversity was achieved by the first window (W1 1Km), an area that had also the second largest LCT diversity. Windows 3, in turn, had the lesser values of all these structural traits. These figures suggest a pattern in which the drivers related to the land-cover types would be more important to determine the structure of the functional maps, than those related to the soil units. It should be noticed that differences in terms LCT diversity among windows are more closely followed by those of EFT diversity in the more detailed classifications. This would indicate that the importance of the vegetation traits represented in the land-cover classification increases with smaller spatial-coverage and pixel-size.

In a different way, when we measure by the coherence index the weight of land-cover and soil-related factors in determining the spatial arrangement of the functional entities, it seems that the soil-related factors have the most pronounced role. It should be noticed that in the three windows the largest indices correspond to the classifications with 1Km^2 pixel-size. This might be due to the coarse spatial-scale at which the soil zonation was performed, but also due to the regional scale at which soil-related functional drivers operate. In summary, while vegetational factors represented in the LCT map exert the primary influence on the variety and frequency-distribution of the functional classes, soil-related factors dominate their spatial configuration. Being so, it is through the changing spatial domain of the causal mechanisms linking vegetation, environment and ecosystem functioning that the effect of spatial-scale on functional patchiness can be understood.

The areas analyzed were different in terms of richness, composition and spatial association of their land-cover and soil units, though fragmentation, which speaks for the dominant grain-size of local landscapes, did not seem to add to their differing landscape configurations. From the three windows, the first and the second are located mainly on the tablelands: the first mostly on the Vacaria tablelands and the second on the Cambará-Tainhas tablelands. The third window, in turn, comprises the Central Depression, most of the Coastal Plain and the southern slope of the *Sierras*. The highly contrasting environments of the third window with more intensive forms of land-use (Table 1), are likely primary contributors to the larger spatial association between land-cover and soil units. This window also showed the lesser functional diversity, which stood in apparent opposition to its greater geomorphic heterogeneity. Yet, excepting in winter, the range of variability of the NDVI seasonal descriptors (Figure 4) was the largest all throughout the annual cycle. This observation reveals that, although the spatial variability of the NDVI mirrored local environmental nonuniformity, the tighter coupling between soils and vegetation modified the group-structure within the NDVI datasets. With increasing pixel-size and/or decreasing spatial-coverage, the sharper image of such a structure rendered a less diverse configuration of functional patches.

In the first and second windows environmental diversity was far less important, vegetation coupling with the soil units was not as tight as in the third window and natural types of vegetation were more extensive. Under those circumstances and in spite of less variable NDVI descriptors (particularly in the second window), a greater refinement of the spatial scale of the analysis revealed a richer scenario of functional heterogeneity. The fact of having a smaller spatial-extent seems to have increased our ability to discriminate functional heterogeneity in the second window, probably by giving more importance to the enhanced NDVI variability in winter. We may then conclude that the quantitative structure and spatial arrangement of the EFTs respond to the group-structure within the NDVI datasets, but that such a structure does not change monotonically with spatial scale.

The modification of spatial-scale parameters did not affect the capability of the EFTs to predict specific LCTs in particular soil units (Table 7). What a more detailed spatial-scale did provide was a closer appreciation of the functional diversity comprised by each land-cover type. In those windows with greater environmental homogeneity, a closer appreciation of functional heterogeneity distinguished a larger number of spatial entities since the classificatory procedure looked for smaller, yet significant, clusters of pixels. This is to say that the functional classification gave more importance to the group-structure determined by the patchy distribution of vegetational drivers. In the highly heterogeneous third window, on the contrary, increased refinement in the space also incremented the dispersion of the NDVI descriptors in relation to the dispersion measured for the complete study area (Figure 4). Under those circumstances, the most evident clusters, products of the tighter association between LCTs and soils, override the classificatory procedure, which leaves undetected the clusters defined at the finer level of functional patchiness.

In general terms, functional patchiness is a dynamic emerging property of the interplay between the vegetation and its environment, an interplay whose key mechanistic linkages also change in relation to the scale of analysis in the space. As such, when we move from broad to fine spatial-scales of analysis, we may define functional heterogeneity on the basis of a more complex array of vegetational and environmental traits, enhancing so the potential diversity and richness of the functional classifications. Yet the opposite may also be true if by down-scaling the comprised environmental heterogeneity becomes as broad and heavily influential as to override the more subtle effect of the vegetational drivers.

Meentemeyer & Box (1987) stated that increasing the extent of a study area would tend to increase the range of variability of a landscape variable. Although this is reasonable to state and has been supported in the literature (see Turner *et al.* 1989, and references therein), the greater dispersion of the NDVI-descriptors in the third window reveals the outstanding effect of environmental variability on the range and degree of variability of a landscape or functional variable. Therefore, if we seek a detailed picture of the functional heterogeneity in a given region, it is appropriate not only to rely on high-resolution and/or spatially-constrained data but also to modify spatial-coverage in order to reduce environmental heterogeneity. Our conclusions are very much in the same spirit of what Turner *et al.* (1989) concluded: "Characterizing the relationships between ecological measurements and the extent or the grain of the data may make it possible to predict or correct for the loss of information with changing spatial-scale."

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Table 1. Site inventory. Dominant types of vegetation / land-use per soil class and landscape unit **in bold**. Areas given in number of pixels with a proximate size of 1 km^2.

			Area		Vegetation / Land-use (% of the soil class in each landscape unit)					
Landscape unit	Area	Soil Types	Pixels	% Landscape Unit	Wetlands	Agriculture	Forestry	Secondary grasslands	Campos	Natural Forests / Shrublands
Coastal Plain	1711	HplUlt	67	4	7	**28**	11	17	**24**	13
		HumEpt	396	23	4	**51**	20	6	0	19
		E.UdEnt	527	31	4	**54**	18	10	0	14
		Alb/Dur	709	41	11	**37**	**28**	13	4	7
		Other	12	1	3	**33**	9	13	5	**37**
Central Depression	1018	HplUlt	963	95	2	10	9	14	**37**	**27**
		Alb/Dur	55	5	11	**32**	15	**21**	11	10
'Serra Geral'	7189	HplUlt	1028	14	1	14	10	11	18	**47**
		DysEpt	169	2	3	2	21	7	12	**55**
		ArgOll	992	14	7	**24**	12	12	7	**39**
		Arg/Ud	4834	67	1	7	15	13	7	**56**
		Other	166	2	3	**21**	15	11	12	**39**
High Tablelands	14299	DysEpt	9259	65	10	1	8	7	32	**43**
		HplOx	3318	23	4	10	5	3	**42**	37
		E.UdEnt	1067	7	7	1	9	7	27	**50**
		Arg/Ud	257	2	2	4	17	9	10	**58**
		Ud/Hum	397	3	1	4	11	9	12	**62**

Table 2. Parameters defining the spatial scale of eight different functional classifications based on MOD13 imagery. Classifications T-1km and T-250m were cropped to fit the three windows (Fig. 2), producing two maps more for each sub-area: T_{W1}-1km and T_{W1}-250m, T_{W2}-1km and T_{W2}-250m, T_{W3}-1km and T_{W3}-250m.

EFT Map	Pixel size	Latitudinal range	Longitudinal range	Coverage (degrees)
T-1km	1 Km^2 (1 Km)	28° to 30°S	51° to 49.5°W	2°Lat x 1.5° Lon Total Area
T-250m	0.0625 Km^2 (250m)	28° to 30°S	51° to 49.5°W	2°Lat x 1.5° Lon Total Area
W1-1km	1 Km^2 (1 Km)	28° to 29°S	51° to 50.5°W	1°Lat x 0.5° Lon Window 1
W1-250m	0.0625 Km^2 (250m)	28° to 29°S	51° to 50.5°W	1°Lat x 0.5° Lon Window 1
W2-1km	1 Km^2 (1 Km)	29° to 29.5°S	50.5° to 50°W	0.5°Lat x 0.5° Lon Window 2
W2-250m	0.0625 Km^2 (250m)	29° to 29.5°S	50.5° to 50°W	0.5°Lat x 0.5° Lon Window 2
W3-1km	1 Km^2 (1 Km)	29.5° to 30°S	50° to 51°W	0.5°Lat x 1° Lon Window 3
W3-250m	0.0625 Km^2 (250m)	29.5° to 30°S	50° to 51°W	0.5°Lat x 1° Lon Window 3

Table 3. Richness (*S*, number of classes) and Diversity (*H*, in nats) of functional classifications with differing spatial-scale parameters. T 1Km and T 250m: classifications obtained from data covering the total extent of the study area, pixel size 1 and 0.0625 Km^2 respectively. W 1Km and W 250m: classifications obtained from data covering specifically the windows, pixel size 1 and 0.0625 Km^2. **Bold** and *italics* type: **highest** and *lowest* values per window.

	W1			
	T 1km	T 250m	W 1km	W 250m
S	*12*	*12*	**21**	20
H	2.32	*2.23*	**2.93**	2.91
	W2			
	T 1km	T 250m	W 1km	W 250m
S	*12*	*12*	22	**24**
H	*1.79*	1.92	2.89	**3.03**
	W3			
	T 1km	T 250m	W 1km	W 250m
S	**12**	**12**	*9*	*9*
H	**1.97**	1.78	*1.71*	1.77

Table 4. Normalized divergence indices (D_{fg}) between EFT maps. Spatial scale parameters per map found in Table 2. **Bold** type: higher divergences per window.

	T_{W1}-250m	W1-1km	W1-250m
W1-1km			**0.7348**
T_{W1}-250m		0.6678	0.5844
T_{W1}-1km	0.6999	0.4539	0.7011
	T_{W2}-250m	W2-1km	W2-250m
W2-1km			**0.6909**
T_{W2}-250m		0.6331	0.4999
T_{W2}-1km	0.6261	0.4173	0.5972
	T_{W3}-250m	W3-1km	W3-250m
W3-1km			0.6904
T_{W3}-250m		**0.6926**	0.4625
T_{W3}-1km	0.6918	0.4050	0.6916

Table 5. EFTs– LCTs (C_{FV}), EFTs – Soil units (C_{FE}) and soil units – LCTs (C_{VS}) coherence indices. **Bold** type: largest coherences per window.

EFT maps	x LCTs (C_{FS})	x Soils (C_{FE})	Soils x LCTs (C_{ES})
TW1-1Km	0.306	0.474	0.254
TW1-250m	**0.315**	0.400	
W1-1Km	0.313	**0.484**	
W1-250m	0.299	0.389	
TW2-1Km	0.360	**0.445**	0.280
TW2-250m	0.351	0.399	
W2-1Km	0.350	0.402	
W2-250m	**0.361**	0.368	
TW3-1Km	0.351	0.483	**0.388**
TW3-250m	0.317	0.421	
W3-1Km	**0.358**	**0.488**	
W3-250m	0.313	0.427	

Table 6. Number of clear associations between ecosystem functional types (EFTs) and land-cover types (LCTs), in each soil unit, according to the deviation of their joint frequencies for random expectation. +D: Positive associations, identifying cases when the presence of a EFT is a strong predictor of the presence of a LCT. –D: Negative associations, identifying cases when a EFT strongly predicts the absence of a LCT. **n**: Number of ecosystem functional types occurring in the soil unit.

	W 250m			W 1Km			T 250m			T 1Km		
	+D	-D	n	+D	-D	n	+D	-D	n	+D	-D	n
	Hapludult											
W3	7	6	8	5	8	8	6	8	10	6	7	10
	Dystrudept											
W1	16	19	20	16	16	20	9	8	12	8	9	11
W2	18	10	24	17	11	22	7	7	12	9	7	12
W3	5	5	8	5	2	5	5	4	5	4	2	5
	Argiudoll											
W2	12	9	13	7	6	10	5	2	6	3	2	4
W3	5	4	9	7	5	9	5	9	12	8	5	12
	Humaquept											
W3	5	3	9	6	5	8	10	6	12	7	5	11
	Hapludox											
W1	15	17	20	12	17	21	8	7	12	7	9	12
	Eutr.Udorthent											
W1	13	6	20	11	6	16	6	3	12	4	1	10
W2	17	11	24	13	5	15	11	2	12	6	1	8
W3	7	6	9	6	5	8	11	6	12	9	4	11
	Albaqualf / Duraqualf											
W3	4	3	9	3	3	7	8	4	12	9	4	12
	Argiudoll / Eutr.Udorthent											
W1	12	13	19	16	8	17	9	10	12	8	8	12
W2	14	10	20	10	9	15	7	7	10	8	7	10
W3	5	5	9	8	7	9	9	9	12	7	7	11
	Dyst.Udorthent / Humaquept											
W1	15	10	17	9	5	10	5	4	6	4	2	5

Table 7. Richness and diversity (Shannon's entropy) of landscape components in the four areas under consideration. S_V and H_V: richness and diversity of land-cover types. S_E and H_E: richness and diversity of soil units.

	W1	W2	W3	T
S_V	7	7	10	10
H_V	1.70	1.78	1.24	1.88
S_E	5	4	7	10
H_E	1.15	0.71	1.68	1.76

Table 8. Fragmentation indices (after Monmonier, 1974) for the three windows under comparison (*Fn*), and for the soil units occurring in the windows (*Fn/k*). The indices refer to the degree of fragmentation of the land-cover types. **Bold** type:: highest soil-specific indices per window.

		Windows					
		1		2		3	
		Mean	SD	Mean	SD	Mean	SD
Fn		0.283	0.131	0.297	0.120	0.267	0.131
Fn!k							
Soil Units	Hapludult	--	--	--	--	0.257	0.128
	Dystrudept	0.300	0.123	0.302	0.118	0.277	0.119
	Argiudoll	--	--	0.257	0.125	0.278	0.133
	Humaquept	--	--	--	--	0.223	0.149
	Hapludox	0.256	0.132	--	--	--	--
	Eut.Udorthent	0.336	0.125	**0.328**	**0.110**	0.249	0.140
	Albaqualf / Duraqualf	--	--	--	--	0.274	0.145
	Argiudoll / E.Udorthent	0.325	0.118	0.286	0.127	**0.280**	**0.120**
	Dys.Udorthent / Humaquept	**0.338**	**0.118**	--	--	--	--

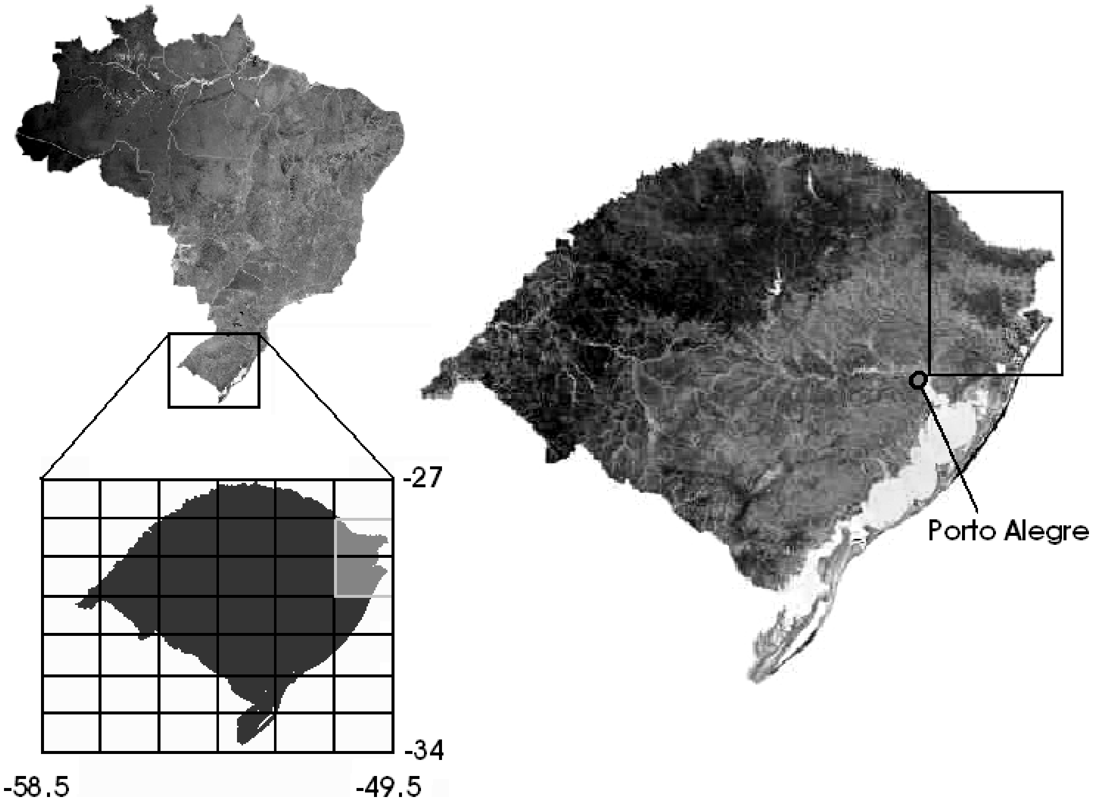

Figure 1. Location of the study area. Grid in lower-left panel in geographical coordinates. Rectangle in the right panel enclosing the study area.

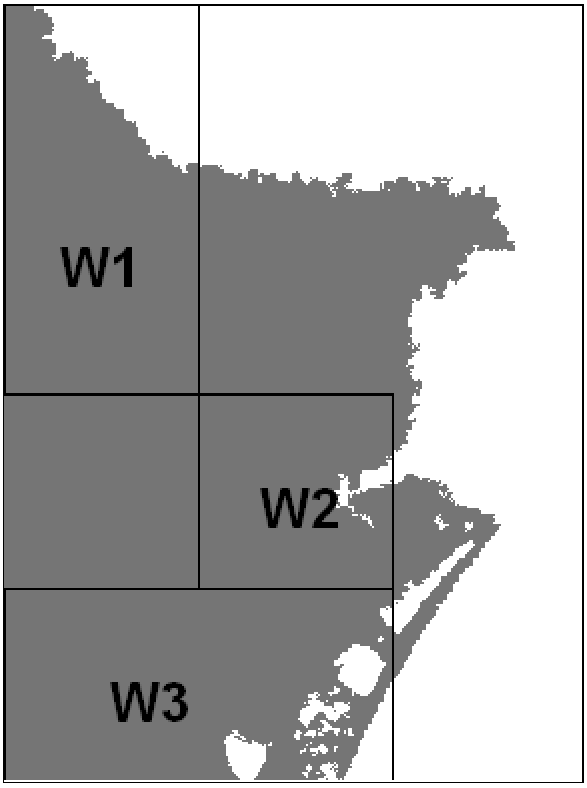

Figure 2. Window 1 (W1), window 2 (W2) and window 3 (W3). The corresponding geographic coordinates appear in Table 2.

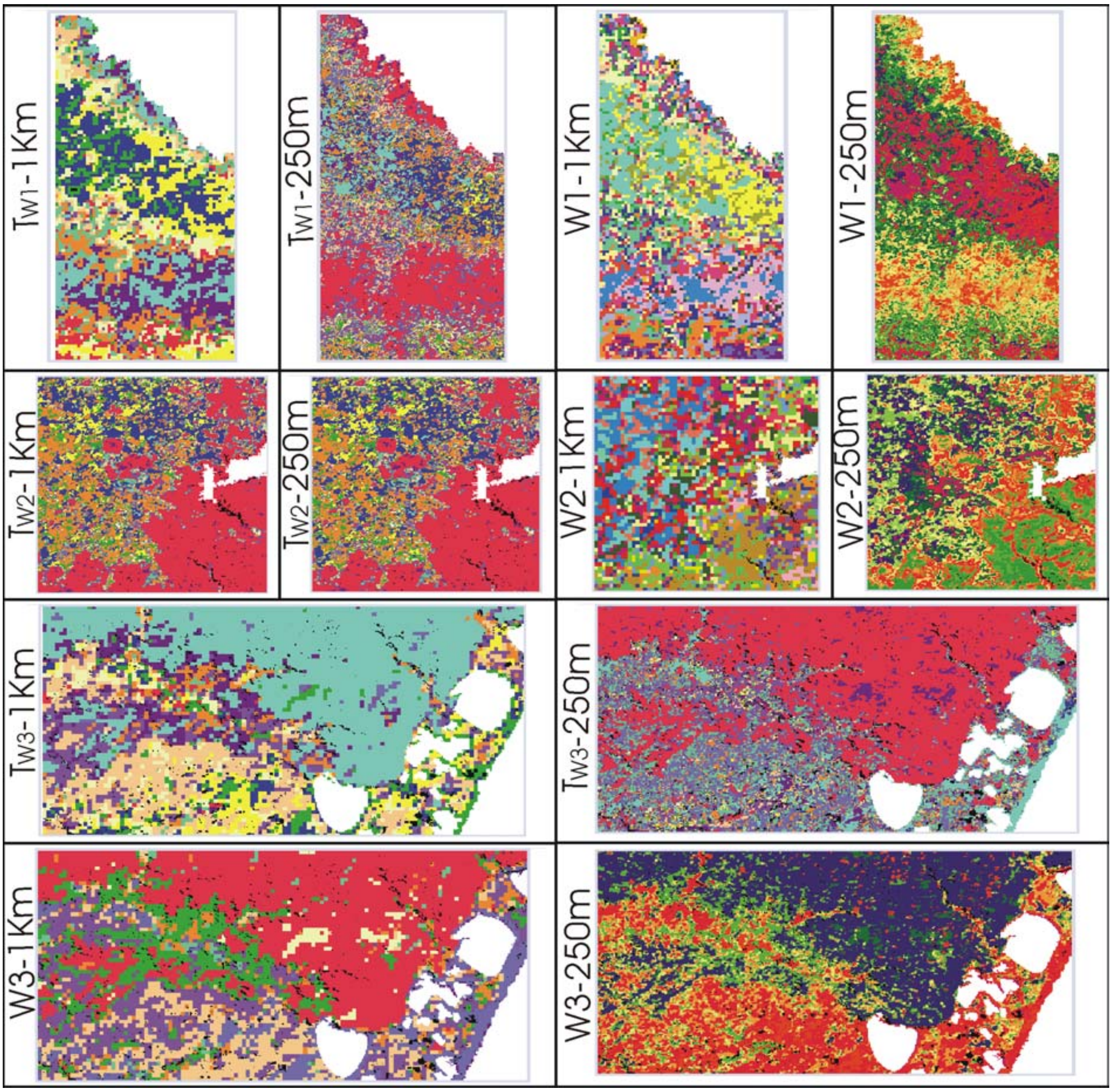

Figure 3. Four EFT classifications per windows, as derived from differing spatial coverage and pixel-sizes. Labels to the left identify the corresponding set of spatial-scale parameters, as these appear in Table 2.

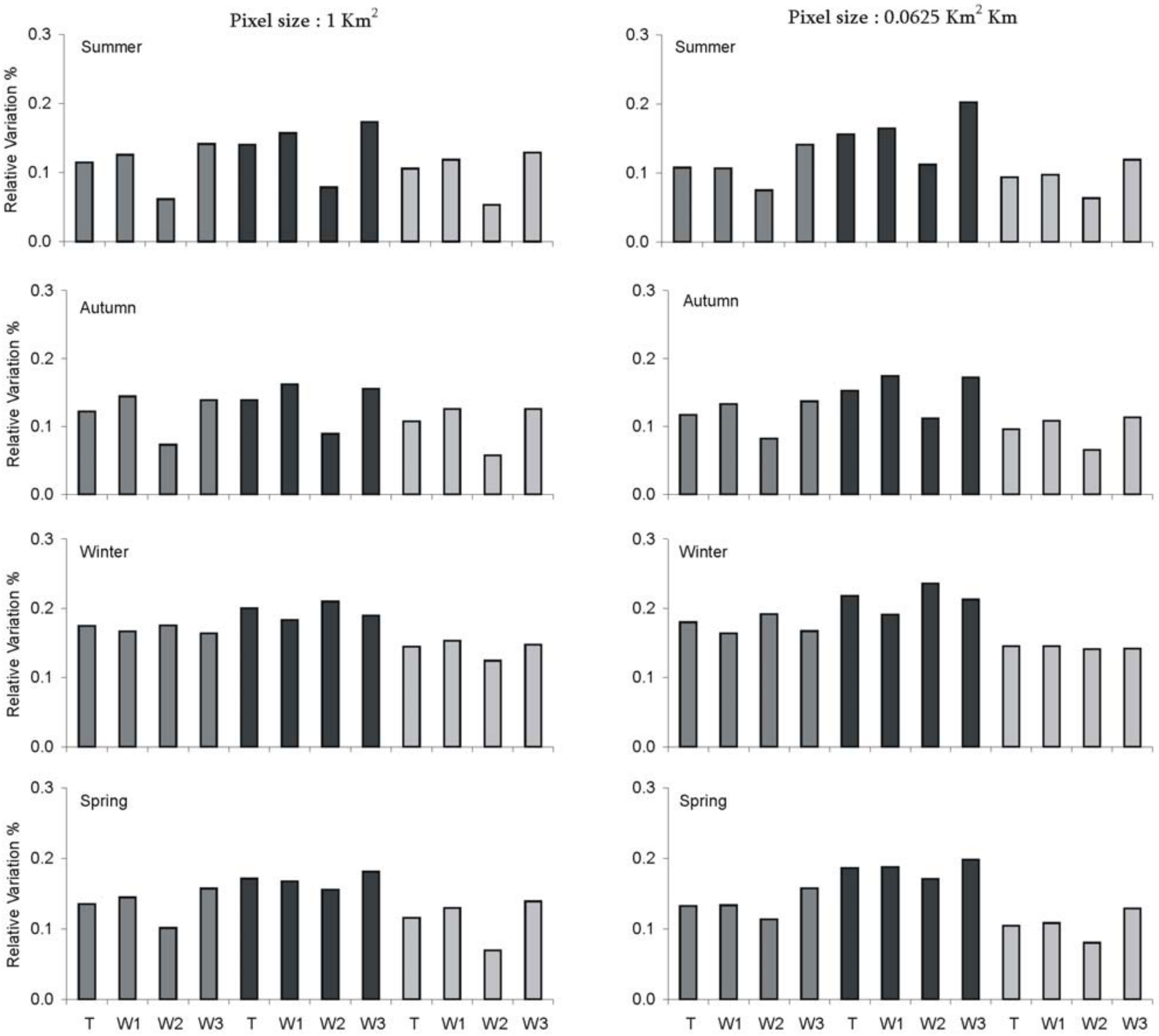

Figure 4. Relative variation coefficients of the spatial averages of each seasonal NDVI descriptor, in relation to the spatial coverage and resolution of the NDVI datasets. ▨ : Mean seasonal NDVI. ■ : Maximum seasonal NDVI. □ : Minimum seasonal NDVI. T: Total Coverage. W1, W2 and W3: window-specific coverage. Pixel-size is indicated at the top of the figure. The relative variation coefficients are the standard deviations expressed as a fraction of the windows averages.

A1. Three-dimensional contingency table with EFT / LCT / Soil types joint frequencies: NDVI-based functional classes in rows, land-cover types in columns and regional soil units in planes. Joint frequencies are given as number of pixels shared. Land-cover types are: **NF** – Natural forest, **CF** – Commercial forest, **Ca** – *Campo*, natural grassland, **SG** – Secondary grassland, **GW** – Grassy wetland, **Shr** – Shrubland, **WB** – permanent water body, **Cr** – Cropland, with growing crop, **Cr(fld)** –cropland, temporally flooded, **Br/ur** – Tilled soil and urban sites.

Window 1

Tw1-1Km

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	1	19	215	217	905	288	787	991	3422
	2	39	126	185	1154	314	593	1027	3438
	3	76	44	15	191	37	154	174	691
	4	46	344	170	586	129	1040	790	3105
	5	5	45	22	81	22	131	112	418
	6	19	127	71	231	57	366	294	1165
	7	1	31	5	40	19	68	82	246
	8	0	0	0	0	0	0	0	0
	9	35	237	129	241	39	639	402	1722
	10	2	70	12	50	2	109	92	337
	11	46	25	123	1761	398	348	956	3657
	12	172	7	7	549	32	45	119	931
Hapludox	1	22	43	25	199	28	181	145	643
	2	297	236	169	2441	315	1069	1632	6159
	3	1780	164	91	2464	192	417	1044	6152
	4	39	397	150	688	132	949	857	3212
	5	2	88	22	147	31	191	188	669
	6	57	397	210	1020	237	1221	1167	4309
	7	49	345	177	1107	196	1026	1189	4089
	8	4	8	5	10	0	24	13	64
	9	17	191	83	185	34	429	277	1216
	10	21	288	104	178	24	469	279	1363
	11	322	125	121	4206	292	728	1553	7347
	12	2484	139	125	6648	417	767	2031	12611
Eutr.Udorthent	1	6	43	23	70	39	113	82	376
	2	1	11	10	51	27	73	56	229
	3	6	37	19	47	40	115	70	334
	4	13	49	34	94	17	161	83	451
	5	15	16	24	40	4	69	34	202
	6	1	15	21	48	11	86	49	231
	7	0	7	12	10	4	48	12	93
	8	0	0	0	0	0	0	0	0

	9	18	35	52	93	24	237	89	548
	10	6	12	29	20	2	119	17	205
	11	1	0	2	12	12	12	6	45
	12	0	0	0	0	0	0	0	0
Argiudoll / Eutr.Udorthent	1	1	5	7	6	0	27	4	50
	2	2	6	8	14	3	21	8	62
	3	11	49	19	59	7	110	48	303
	4	96	188	245	276	24	773	260	1862
	5	4	22	20	57	3	64	36	206
	6	20	182	102	185	38	371	237	1135
	7	10	58	61	131	14	170	86	530
	8	14	39	38	18	4	103	55	271
	9	416	860	866	928	66	3267	863	7266
	10	332	1066	1121	666	47	3713	861	7806
	11	0	0	1	0	1	3	0	5
	12	0	0	2	17	1	9	11	40
Dyst.Udorthent / Humaquept	1	0	0	0	2	0	2	1	5
	2	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	4	24	28	56	60	1	146	25	340
	5	0	0	0	0	0	0	0	0
	6	8	8	19	25	1	65	18	144
	7	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0
	9	43	23	45	55	4	146	24	340
	10	15	23	29	12	0	84	8	171
	11	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0

TW1-250m

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	1	34	436	143	315	46	933	569	2476
	2	8	68	54	185	63	218	220	816
	3	19	57	93	561	144	327	492	1693
	4	70	63	185	1508	352	409	952	3539
	5	64	432	231	821	201	1422	1131	4302
	6	7	45	27	124	59	148	209	619
	7	20	96	88	386	102	418	409	1519
	8	11	44	55	337	101	204	326	1078
	9	58	14	3	71	5	21	29	201
	10	41	2	4	105	5	9	25	191
	11	11	7	16	198	68	57	152	509
	12	117	7	57	1178	191	114	525	2189

Hapludox	1	62	967	209	616	80	1503	1126	4563
	2	25	22	9	136	19	64	75	350
	3	88	23	31	639	44	142	316	1283
	4	498	61	108	3670	256	624	1383	6600
	5	70	360	220	1045	219	1312	1313	4539
	6	43	113	59	382	70	346	431	1444
	7	162	356	207	1501	257	1325	1381	5189
	8	147	195	211	1850	308	1030	1348	5089
	9	1090	144	49	1139	103	226	472	3223
	10	1978	84	79	2058	136	228	728	5291
	11	164	35	28	919	74	132	326	1678
	12	799	61	72	5338	332	539	1476	8617
Eutr. Udorthent	1	17	84	71	107	19	347	117	762
	2	5	25	14	32	17	91	49	233
	3	0	2	13	38	27	46	44	170
	4	2	3	8	48	27	34	48	170
	5	16	67	63	141	46	290	157	780
	6	11	8	18	18	7	94	20	176
	7	5	22	25	56	13	72	35	228
	8	5	10	10	21	12	30	12	100
	9	7	7	3	9	1	26	9	62
	10	9	22	7	3	4	7	0	52
	11	0	0	1	8	2	3	5	19
	12	1	0	1	6	6	7	2	23
Argiudoll / Eutr. Udorthent	1	635	1871	1821	1213	83	6570	1611	13804
	2	5	8	17	22	0	40	6	98
	3	1	6	6	10	3	12	9	47
	4	2	8	9	15	5	19	7	65
	5	184	320	382	603	52	1227	476	3244
	6	8	34	32	62	7	97	39	279
	7	40	96	84	222	26	308	154	930
	8	7	38	64	138	28	125	80	480
	9	24	91	78	62	3	234	84	576
	10	5	4	4	9	1	35	2	60
	11	1	1	4	2	1	6	4	19
	12	0	2	0	5	0	7	1	15
Dyst.Udorthent / Humaquept	1	53	45	77	49	1	236	34	495
	2	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0	0	1	0	0	0	1
	5	35	34	61	82	5	177	32	426
	6	0	0	0	1	0	0	0	1
	7	2	3	10	14	0	26	9	64
	8	0	0	1	7	0	4	1	13
	9	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0

	11	0	0	0	0	0	0	0	0
	12	0	0	0	0	0	0	0	0

W1-1Km

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	1	10	68	103	514	152	248	512	1607
	2	7	21	16	222	47	51	130	494
	3	5	34	30	122	59	139	168	557
	4	24	251	199	830	277	915	1068	3564
	5	6	28	16	43	8	76	56	233
	6	16	150	77	294	84	449	412	1482
	7	7	17	36	360	60	114	222	816
	8	39	5	63	792	182	164	403	1648
	9	2	36	90	712	257	257	617	1971
	10	205	3	4	255	16	21	68	572
	11	26	4	9	587	27	28	128	809
	12	13	118	50	202	38	344	296	1061
	13	25	190	106	353	67	566	393	1700
	14	3	39	9	30	8	73	44	206
	15	11	22	29	44	4	108	66	284
	16	20	128	68	139	24	410	215	1004
	17	1	11	4	21	0	46	21	104
	18	0	0	0	0	0	0	0	0
	19	12	130	41	86	12	222	159	662
	20	2	15	5	14	1	34	22	93
	21	26	1	1	169	14	15	39	265
Hapludox	1	110	89	93	645	113	369	461	1880
	2	159	137	82	1212	156	590	882	3218
	3	322	196	91	908	126	437	753	2833
	4	4	21	6	99	16	99	75	320
	5	40	164	92	628	122	560	641	2247
	6	44	247	151	797	177	1042	856	3314
	7	121	113	74	1497	162	547	837	3351
	8	56	16	25	813	58	107	309	1384
	9	0	3	4	98	7	24	48	184
	10	3051	168	118	4315	336	606	1673	10267
	11	611	47	47	4358	206	458	1048	6775
	12	19	247	73	418	92	498	591	1938
	13	6	88	43	200	30	259	186	812
	14	31	279	115	425	81	685	560	2176
	15	19	189	63	265	41	318	316	1211
	16	12	134	61	108	20	262	179	776
	17	0	3	0	2	0	9	13	27
	18	2	36	13	11	1	60	18	141
	19	2	104	29	44	6	137	95	417
	20	14	111	49	51	5	196	98	524

	21	503	29	53	2399	143	208	736	4071
Eutr. Udorthent	1	2	6	8	18	27	31	29	121
	2	0	0	1	1	1	0	0	3
	3	1	12	9	49	15	77	51	214
	4	7	42	28	80	50	167	108	482
	5	1	5	9	8	0	38	6	67
	6	0	4	5	40	9	36	37	131
	7	0	0	0	0	0	0	0	0
	8	0	1	2	3	4	6	7	23
	9	1	3	4	28	17	21	11	85
	10	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0
	12	17	53	39	81	21	189	83	483
	13	10	49	42	81	17	163	85	447
	14	14	10	35	16	2	79	7	163
	15	4	3	9	16	4	31	11	78
	16	1	17	6	16	5	58	24	127
	17	4	4	4	5	4	13	10	44
	18	0	0	0	0	0	0	0	0
	19	4	12	15	35	4	69	20	159
	20	1	4	10	8	0	55	9	87
	21	0	0	0	0	0	0	0	0
Argiudoll / E. Udorthent	1	0	6	3	22	1	27	14	73
	2	0	3	9	7	0	17	3	39
	3	9	24	28	51	1	106	25	244
	4	1	9	6	1	0	17	0	34
	5	8	57	24	104	14	82	84	373
	6	6	25	16	42	10	100	62	261
	7	0	0	5	12	4	1	3	25
	8	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0
	10	1	0	0	13	0	9	1	24
	11	0	0	0	0	0	0	0	0
	12	18	81	72	130	15	282	136	734
	13	51	101	106	144	18	277	122	819
	14	49	125	144	226	34	423	190	1191
	15	74	245	230	288	27	766	265	1895
	16	83	240	248	276	16	927	237	2027
	17	53	172	118	132	10	438	154	1077
	18	14	61	71	34	1	189	37	407
	19	321	643	657	533	31	2570	624	5379
	20	218	683	753	342	26	2400	512	4934
	21	0	0	0	0	0	0	0	0

D.Udorthent / Humaquept	1	0	0	0	0	0	0	0	0
	2	0	0	0	0	0	0	0	0
	3	0	0	0	0	0	0	0	0
	4	0	0	0	1	0	0	0	1
	5	0	0	0	0	0	0	0	0
	6	8	8	15	10	0	28	1	70
	7	0	0	0	0	0	0	0	0
	8	0	0	0	0	0	0	0	0
	9	0	0	0	0	0	0	0	0
	10	0	0	0	0	0	0	0	0
	11	0	0	0	0	0	0	0	0
	12	4	3	14	22	1	32	4	80
	13	8	8	16	31	1	63	36	163
	14	5	2	7	9	0	24	1	48
	15	18	18	20	33	2	87	8	186
	16	27	23	55	37	2	137	15	296
	17	0	0	1	1	0	3	0	5
	18	0	0	0	0	0	0	0	0
	19	13	3	9	7	0	34	7	73
	20	7	17	12	3	0	35	4	78
	21	0	0	0	0	0	0	0	0

W1-250m

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	1	53	21	40	246	101	117	202	780
	2	12	4	7	54	10	9	40	136
	3	16	20	21	92	26	80	112	367
	4	25	208	123	412	103	640	590	2101
	5	44	43	55	378	103	275	406	1304
	6	15	28	48	262	78	125	244	800
	7	38	219	216	952	305	917	1089	3736
	8	4	38	15	58	9	140	74	338
	9	26	129	82	229	49	472	284	1271
	10	3	64	11	45	12	104	72	311
	11	15	86	40	101	15	236	142	635
	12	11	116	28	120	17	325	204	821
	13	6	94	36	54	12	176	88	466
	14	3	14	6	5	3	17	15	63
	15	0	11	6	4	0	27	13	61
	16	2	125	28	48	7	178	121	509
	17	32	23	80	893	209	208	584	2029
	18	15	13	65	728	153	130	375	1479
	19	54	0	8	369	21	20	86	558
	20	86	15	41	739	104	84	298	1367

Hapludox	1	285	23	44	1174	95	205	457	2283
	2	98	32	24	1254	78	242	435	2163
	3	976	224	110	1261	170	684	874	4299
	4	151	227	148	775	166	884	891	3242
	5	464	163	141	1661	237	817	1105	4588
	6	212	81	108	1147	158	462	760	2928
	7	81	63	69	496	92	350	419	1570
	8	28	145	69	469	96	438	502	1747
	9	49	136	93	421	75	441	427	1642
	10	55	181	56	276	51	454	400	1473
	11	34	248	59	282	27	511	418	1579
	12	16	217	70	151	26	366	274	1120
	13	10	123	34	95	10	183	133	588
	14	8	39	7	42	7	91	64	258
	15	2	79	13	28	1	98	59	280
	16	5	310	37	75	3	304	198	932
	17	488	24	51	1909	157	226	679	3534
	18	151	24	43	1769	115	222	592	2916
	19	400	12	19	2971	113	166	537	4218
	20	1613	70	87	3037	221	327	1151	6506
Eutr.Udorthent	1	0	1	5	20	10	15	17	68
	2	0	0	0	0	0	1	3	4
	3	3	1	9	6	2	19	8	48
	4	6	26	36	81	31	149	81	410
	5	2	9	9	17	12	42	25	116
	6	8	1	9	18	3	19	7	65
	7	9	42	38	87	51	162	102	491
	8	4	8	14	20	3	45	15	109
	9	5	34	25	50	11	136	42	303
	10	9	8	11	17	1	34	18	98
	11	4	19	10	19	5	70	24	151
	12	8	30	21	35	13	112	47	266
	13	2	21	8	29	6	70	23	159
	14	3	3	1	1	0	10	2	20
	15	0	0	5	5	1	4	1	16
	16	3	17	22	28	2	112	41	225
	17	1	4	2	24	17	28	22	98
	18	0	1	1	25	9	5	17	58
	19	0	0	0	0	1	0	0	1
	20	0	0	0	3	2	0	3	8
Argiudoll / E.Udorthent	1	2	0	5	3	0	3	3	16
	2	1	1	4	19	1	6	1	33
	3	9	29	32	66	15	103	53	307
	4	52	95	103	163	16	312	129	870
	5	3	23	42	88	11	78	49	294
	6	5	11	20	73	7	52	36	204

	7	23	38	38	101	8	162	72	442
	8	29	66	74	144	19	203	95	630
	9	136	206	250	417	36	881	297	2223
	10	43	60	90	82	12	238	70	595
	11	94	206	288	236	18	920	247	2009
	12	127	297	296	225	20	1041	268	2274
	13	177	466	505	290	22	1819	439	3718
	14	39	106	97	96	5	353	98	794
	15	10	120	82	76	3	359	114	764
	16	156	747	562	268	12	2093	490	4328
	17	0	3	0	3	1	4	3	14
	18	0	1	2	4	1	1	2	11
	19	0	0	0	0	0	0	0	0
	20	0	0	0	3	1	3	3	10
D.Udorthent / Humaquept	1	0	0	0	0	0	2	0	2
	2	0	0	0	0	0	0	0	0
	3	0	0	1	3	1	3	1	9
	4	9	14	13	17	1	34	4	92
	5	0	1	3	5	0	11	2	22
	6	0	0	0	0	0	0	2	2
	7	8	8	18	38	1	54	11	138
	8	2	4	4	2	0	7	1	20
	9	27	19	41	43	3	126	26	285
	10	2	0	2	4	0	3	0	11
	11	9	6	11	13	0	31	6	76
	12	13	7	19	10	0	74	11	134
	13	11	7	22	6	0	52	6	104
	14	2	0	0	4	0	8	0	14
	15	1	0	0	0	0	2	0	3
	16	6	16	15	6	0	36	4	83
	17	0	0	0	0	0	0	1	1
	18	0	0	0	3	0	0	1	4
	19	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0

Window 2

Tw2-1Km

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	13	10	78	192	606	399	346	570	2201
	14	40	177	480	1481	1112	642	1593	5525
	15	12	147	84	388	216	253	346	1446
	16	8	392	124	384	256	576	480	2220
	17	3	187	57	176	132	241	260	1056
	18	1	154	20	107	59	143	123	607
	19	6	140	31	122	89	166	193	747
	20	2	170	5	55	10	151	76	469
	21	0	143	16	55	55	172	131	572
	22	78	2399	261	488	143	2610	1231	7210
	23	56	204	1442	5502	3029	1874	4354	16461
	24	16	30	81	379	255	110	374	1245
Argiudoll	13	0	0	0	0	0	0	0	0
	14	0	0	0	0	0	0	0	0
	15	0	0	0	0	0	0	0	0
	16	0	0	0	0	0	9	0	9
	17	0	0	0	0	0	0	0	0
	18	0	0	0	0	0	0	0	0
	19	0	0	0	0	0	0	0	0
	20	0	16	5	1	0	8	2	32
	21	8	1	2	0	0	16	0	27
	22	98	211	182	31	8	646	63	1239
	23	0	0	0	0	0	0	0	0
	24	0	0	0	0	0	0	0	0
Eut.Udorthent	13	0	13	14	52	21	61	50	211
	14	1	11	15	20	4	66	16	133
	15	0	0	0	4	9	2	4	19
	16	0	17	8	31	6	19	28	109
	17	0	0	0	0	0	0	0	0
	18	0	8	2	17	5	7	20	59
	19	0	0	0	0	0	0	0	0
	20	0	0	0	0	0	0	0	0
	21	0	0	0	0	0	0	0	0
	22	0	15	0	4	1	20	1	41
	23	3	14	148	462	232	333	273	1465
	24	1	2	8	16	6	14	17	64
Argiudoll / Eut.Udorthent	13	0	1	2	1	5	1	6	16
	14	0	0	4	1	13	0	6	24
	15	1	7	3	2	4	8	3	28
	16	0	21	8	4	16	10	21	80
	17	0	51	9	25	11	40	44	180

	18	0	0	0	0	9	0	4	13
	19	0	0	0	2	0	0	7	9
	20	12	39	33	12	1	80	22	199
	21	0	23	5	32	5	31	42	138
	22	455	1507	936	420	105	3221	709	7353
	23	0	0	0	0	0	0	0	0
	24	0	0	0	0	0	0	0	0

Tw2-250m

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	13	82	3133	318	800	257	3214	1689	9493
	14	4	49	71	200	167	165	199	855
	15	6	53	316	986	646	477	812	3296
	16	39	126	798	2620	1690	904	2247	8424
	17	11	279	136	503	304	623	621	2477
	18	3	119	53	240	150	249	304	1118
	19	7	83	68	206	111	214	235	924
	20	9	89	88	264	208	205	333	1196
	21	8	185	17	75	47	158	122	612
	22	16	22	22	129	68	31	131	419
	23	5	17	216	851	568	282	724	2663
	24	42	66	690	2869	1539	762	2314	8282
Argiudoll	13	90	226	185	32	8	646	65	1252
	14	0	0	0	0	0	2	0	2
	15	0	0	0	0	0	0	0	0
	16	0	0	0	0	0	0	0	0
	17	3	0	1	0	0	25	0	29
	18	0	0	0	0	0	0	0	0
	19	7	0	0	0	0	3	0	10
	20	5	0	0	0	0	1	0	6
	21	1	2	3	0	0	2	0	8
	22	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0
	24	0	0	0	0	0	0	0	0
Eu.Udorthent	13	1	43	7	19	2	36	35	143
	14	0	1	11	16	4	28	9	69
	15	1	2	17	61	27	86	31	225
	16	0	4	21	77	35	71	46	254
	17	1	12	9	28	12	42	22	126
	18	0	1	1	11	5	15	8	41
	19	0	0	4	22	8	35	11	80
	20	0	2	5	3	2	11	5	28
	21	0	4	1	3	0	4	0	12
	22	0	0	1	5	5	1	1	13
	23	1	7	21	59	24	73	47	232
	24	6	27	98	302	160	128	194	915

Argiudoll / Eu.Udorthent	13	451	1542	956	427	104	3220	739	7439
	14	0	5	2	3	6	1	13	30
	15	0	2	7	1	15	0	3	28
	16	0	4	1	2	19	4	14	44
	17	9	36	11	24	9	46	31	166
	18	0	20	3	16	6	19	22	86
	19	3	3	1	2	2	17	9	37
	20	0	3	0	5	3	9	8	28
	21	5	34	19	19	5	75	25	182
	22	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0
	24	2	6	1	0	2	1	0	12

W2-1km

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	22	2	3	151	620	320	98	422	1616
	23	13	21	552	1857	1037	473	1346	5299
	24	1	10	2	15	28	9	24	89
	25	26	142	396	1142	810	666	1176	4358
	26	3	55	101	277	236	219	405	1296
	27	2	44	61	147	150	121	179	704
	28	14	313	155	573	370	540	693	2658
	29	10	11	217	907	505	262	729	2641
	30	28	42	214	1019	604	201	828	2936
	31	17	80	321	1242	678	575	1024	3937
	32	28	135	187	834	471	400	858	2913
	33	46	363	105	66	10	503	86	1179
	34	7	180	70	54	5	372	100	788
	35	4	164	19	21	10	263	99	580
	36	0	173	4	39	6	159	94	475
	37	6	190	14	31	8	187	93	529
	38	0	476	9	57	21	380	205	1148
	39	5	208	15	67	33	174	184	686
	40	4	393	25	121	32	369	255	1199
	41	3	274	9	62	18	231	139	736
	42	12	810	86	404	262	831	592	2997
	43	1	134	80	188	141	251	200	995
Argiudoll	22	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0
	24	0	0	0	0	0	0	0	0
	25	0	0	0	0	0	0	0	0
	26	0	0	0	0	0	0	0	0
	27	0	0	0	0	0	0	0	0
	28	0	0	0	0	0	0	0	0
	29	0	0	0	0	0	0	0	0
	30	0	0	0	0	0	0	0	0

	31	0	0	0	0	0	0	0	0
	32	0	0	0	0	0	0	0	0
	33	26	102	102	18	4	338	47	637
	34	1	26	9	4	0	60	7	107
	35	13	41	15	2	0	64	5	140
	36	2	18	7	1	4	13	0	45
	37	0	1	4	0	0	10	1	16
	38	3	10	12	3	0	17	2	47
	39	6	3	3	1	0	22	0	35
	40	9	15	23	2	0	82	3	134
	41	44	12	13	1	0	53	0	123
	42	2	0	1	0	0	20	0	23
	43	0	0	0	0	0	0	0	0
E.Udorthent	22	0	0	0	0	0	0	0	0
	23	0	3	37	101	66	87	86	380
	24	0	2	4	8	3	6	12	35
	25	0	8	14	74	21	78	33	228
	26	1	8	6	12	9	36	8	80
	27	0	0	0	0	0	0	0	0
	28	0	4	5	7	5	21	18	60
	29	0	3	31	76	47	41	61	259
	30	2	5	30	72	51	34	53	247
	31	1	4	26	136	38	120	50	375
	32	1	1	27	63	24	42	32	190
	33	0	0	0	0	0	0	0	0
	34	0	0	0	0	0	0	0	0
	35	0	0	0	0	0	0	0	0
	36	0	1	0	0	0	1	0	2
	37	0	0	0	0	0	0	0	0
	38	0	0	0	0	0	0	0	0
	39	0	0	0	0	0	0	1	1
	40	0	9	0	1	0	6	0	16
	41	0	5	0	3	1	13	1	23
	42	0	17	4	20	4	13	23	81
	43	0	10	11	33	15	24	31	124
Argiudoll / E.Udorthent	22	0	0	0	0	0	0	0	0
	23	0	0	0	0	0	0	0	0
	24	0	0	0	0	0	0	0	0
	25	0	0	0	0	2	0	0	2
	26	0	1	2	1	5	1	6	16
	27	0	0	3	1	9	0	3	16
	28	0	10	1	14	6	5	22	58
	29	0	0	0	0	0	0	0	0
	30	0	0	0	0	0	0	0	0
	31	0	0	0	0	0	0	0	0
	32	0	0	0	0	0	0	0	0

	33	159	560	371	124	30	1255	232	2731
	34	90	288	155	63	23	550	121	1290
	35	58	205	160	80	16	492	94	1105
	36	28	107	74	23	3	239	56	530
	37	16	68	38	17	3	101	23	266
	38	8	19	29	18	5	80	16	175
	39	26	59	52	28	4	110	38	317
	40	18	67	39	34	7	188	49	402
	41	62	132	52	37	11	264	84	642
	42	3	129	22	53	34	103	108	452
	43	0	4	2	6	11	3	12	38

W2-250m

	EFTs	Cr	CF	SG	Ca	GW	NF	Sh	Total
Dystrudept	21	13	7	441	1651	942	330	1344	4728
	22	12	4	115	435	223	76	338	1203
	23	8	7	130	510	261	117	301	1334
	24	5	56	236	732	588	313	781	2711
	25	11	46	102	413	271	178	421	1442
	26	8	37	178	512	404	228	462	1829
	27	38	693	139	59	17	542	145	1633
	28	20	440	58	96	24	699	245	1582
	29	2	7	132	615	280	111	386	1533
	30	14	39	323	1053	740	535	911	3615
	31	7	32	99	361	206	232	267	1204
	32	4	30	134	380	268	200	384	1400
	33	11	225	193	624	485	687	788	3013
	34	3	138	111	342	208	386	375	1563
	35	2	499	5	57	12	213	122	910
	36	6	293	5	58	13	282	174	831
	37	0	164	5	26	9	114	74	392
	38	4	333	29	131	20	409	278	1204
	39	1	127	11	48	12	159	95	453
	40	6	289	22	138	48	413	258	1174
	41	5	333	50	208	87	332	280	1295
	42	10	371	86	342	183	529	521	2042
	43	11	25	152	632	334	118	497	1769
	44	31	26	37	320	120	81	284	899
Argiudoll	21	0	0	0	0	0	0	0	0
	22	0	0	0	0	0	0	0	0
	23	1	0	0	0	0	0	0	1
	24	0	0	0	0	0	0	0	0
	25	0	0	0	0	0	0	0	0
	26	0	0	0	0	0	0	0	0
	27	24	123	82	16	1	272	27	545
	28	10	51	36	6	4	92	14	213

	29	0	0	0	0	0	0	0	0
	30	0	0	0	0	0	0	0	0
	31	0	0	0	0	0	0	0	0
	32	0	0	0	0	0	0	0	0
	33	10	0	0	0	0	6	0	16
	34	1	0	0	0	0	9	0	10
	35	1	1	2	0	0	7	2	13
	36	4	12	16	3	2	32	2	71
	37	3	5	2	1	0	12	5	28
	38	7	12	16	3	1	72	6	117
	39	4	8	8	1	0	37	4	62
	40	13	7	7	0	0	52	3	82
	41	4	1	7	1	0	17	0	30
	42	24	8	13	1	0	71	2	119
	43	0	0	0	0	0	0	0	0
	44	0	0	0	0	0	0	0	0
Eu.Udorthent	21	0	1	31	71	42	32	50	227
	22	1	1	11	45	27	11	25	121
	23	0	0	6	19	12	6	9	52
	24	0	0	18	71	28	42	26	185
	25	0	0	22	48	25	19	37	151
	26	0	1	12	59	21	36	20	149
	27	0	15	0	2	0	6	5	28
	28	0	3	0	1	0	6	0	10
	29	0	3	1	9	5	7	4	29
	30	1	10	27	105	49	106	87	385
	31	0	0	9	21	17	35	17	99
	32	0	2	16	31	9	38	25	121
	33	2	4	10	25	14	63	20	138
	34	0	4	13	31	9	54	25	136
	35	0	1	0	3	0	1	2	7
	36	0	5	0	0	0	2	4	11
	37	0	0	0	1	0	0	1	2
	38	0	8	3	3	0	11	4	29
	39	0	1	1	0	1	0	2	5
	40	0	10	1	7	1	11	8	38
	41	1	7	1	10	3	10	10	42
	42	0	4	6	12	6	21	12	61
	43	0	0	5	29	13	4	15	66
	44	0	0	2	3	2	1	1	9
Argiudoll / E.Udorthent	21	0	0	0	0	1	0	0	1
	22	0	0	0	0	0	1	0	1
	23	0	0	0	0	0	0	0	0
	24	0	1	6	3	18	0	5	33
	25	0	0	0	1	2	1	1	5

26	0	2	0	0	3	1	4	10
27	135	706	369	126	23	1061	166	2586
28	103	323	261	109	29	963	217	2005
29	0	0	0	0	0	0	0	0
30	0	0	1	1	5	0	2	9
31	0	2	1	0	4	0	2	9
32	0	1	0	0	0	1	1	3
33	3	36	11	22	17	59	55	203
34	3	19	3	12	2	36	16	91
35	10	50	22	10	2	64	24	182
36	38	85	51	26	8	213	48	469
37	14	28	22	15	5	66	14	164
38	38	133	97	36	9	315	87	715
39	27	46	35	21	12	129	46	316
40	38	72	63	37	8	184	52	454
41	18	28	12	10	2	61	22	153
42	41	117	46	70	19	236	102	631
43	0	0	0	0	0	0	0	0
44	0	0	0	0	0	0	0	0

Window 3

Tw3 1km

	EFTs	PW	Cr(Fld)	Cr	CF	SG	Ca	GW	NF	Sh	B/U	Total
Hapludult	25	0	0	34	28	15	11	30	14	1	4	137
	26	0	4	280	124	403	783	58	290	1	32	1975
	27	0	7	121	123	92	186	26	183	5	42	785
	28	0	0	261	133	146	375	32	639	15	1	1602
	29	0	6	529	471	451	2020	101	1973	61	32	5644
	30	0	0	57	33	30	37	17	144	2	2	322
	31	0	33	973	422	1258	2873	248	1449	25	84	7365
	32	0	0	6	31	28	60	0	146	13	0	284
	33	0	0	427	317	406	943	13	1854	82	13	4055
	34	0	0	413	982	918	869	0	4137	416	4	7739
	35	0	19	253	174	237	574	61	146	1	75	1540
	36	0	13	106	103	62	178	24	94	2	29	611
Dystrudept	25	0	0	0	0	0	0	0	0	0	0	0
	26	0	0	0	0	0	0	0	0	0	0	0
	27	0	0	0	15	0	0	0	1	0	0	16
	28	0	0	0	0	0	0	0	0	0	0	0
	29	0	0	0	13	1	2	0	19	4	0	39
	30	0	0	0	0	0	0	0	0	0	0	0
	31	0	0	0	0	0	0	0	0	0	0	0
	32	0	0	6	95	7	7	0	62	30	0	207
	33	0	0	0	0	0	0	0	2	0	0	2
	34	0	0	202	1153	413	207	60	1425	395	0	3855
	35	0	0	0	0	0	0	0	0	0	0	0
	36	0	0	0	0	0	0	0	0	0	0	0
Argiudoll	25	1	22	81	60	29	8	131	71	0	18	421
	26	0	8	221	148	177	124	156	143	0	35	1012
	27	0	43	104	70	23	29	127	131	0	39	566
	28	0	9	449	97	126	125	88	450	11	13	1368
	29	0	1	382	77	142	166	129	366	6	49	1318
	30	0	0	68	16	24	13	42	70	0	3	236
	31	0	8	434	155	217	164	201	268	1	50	1498
	32	0	0	4	15	28	7	0	96	10	10	170
	33	0	10	348	54	124	160	99	539	21	8	1363
	34	0	0	323	588	526	161	1	2107	224	20	3950
	35	0	2	120	60	39	25	33	53	0	18	350
	36	0	4	62	61	22	54	32	41	0	19	295
Humaquept	25	0	14	1	11	1	0	7	3	0	17	54
	26	1	54	30	74	7	0	24	42	0	71	303
	27	10	34	43	216	8	0	19	84	0	527	941
	28	1	10	17	76	14	0	12	20	0	77	227
	29	1	19	69	85	41	0	8	97	0	142	462

	30	0	21	2	67	0	0	4	11	0	87	192
	31	1	79	60	260	22	0	24	45	0	278	769
	32	0	3	0	16	1	0	0	1	0	6	27
	33	0	37	3	1	0	0	9	4	0	19	73
	34	0	0	0	0	0	0	0	0	0	0	0
	35	3	27	18	183	5	0	20	20	0	106	382
	36	0	20	9	127	5	0	10	29	0	130	330
Eutr.Udorthent	25	0	0	0	11	0	0	0	0	0	1	12
	26	0	7	15	101	6	0	1	10	0	82	222
	27	20	59	132	338	50	8	8	118	0	646	1379
	28	2	11	96	18	44	5	2	59	0	18	255
	29	3	25	162	178	62	3	25	102	0	209	769
	30	0	1	0	9	12	0	0	11	1	13	47
	31	3	27	170	197	51	5	26	104	1	288	872
	32	0	1	12	14	18	2	0	79	5	18	149
	33	0	0	0	0	0	0	0	0	0	0	0
	34	0	2	8	55	27	23	1	40	0	27	183
	35	19	60	163	410	36	4	13	108	0	477	1290
	36	3	28	27	225	13	0	5	26	0	263	590
Albaqualf / Duraqualf	25	0	28	5	8	0	0	7	21	0	7	76
	26	1	49	310	457	227	67	164	105	0	223	1603
	27	5	59	156	554	55	17	102	38	0	259	1245
	28	0	3	18	4	2	11	21	29	0	1	89
	29	0	29	240	125	149	108	136	211	0	49	1047
	30	0	3	10	4	6	10	4	10	0	2	49
	31	0	114	984	800	928	321	418	331	0	382	4278
	32	0	0	0	3	0	6	0	13	0	3	25
	33	0	1	6	5	3	0	4	20	0	4	43
	34	0	0	2	2	4	3	0	12	0	0	23
	35	2	74	560	769	203	72	321	99	0	377	2477
	36	2	112	240	771	78	59	158	76	0	345	1841
Argiudoll / E.Udorthent	25	0	0	0	0	0	0	0	0	0	0	0
	26	0	0	5	5	3	2	0	21	0	1	37
	27	5	2	77	118	110	43	13	260	34	114	776
	28	0	0	129	27	76	24	2	191	4	30	483
	29	0	10	136	72	98	39	5	220	16	89	685
	30	0	0	4	9	5	6	0	33	6	3	66
	31	2	0	47	30	44	12	5	98	4	55	297
	32	0	0	28	104	93	46	12	268	28	7	586
	33	0	0	134	177	218	133	7	735	83	0	1487
	34	0	0	1224	3723	3179	880	68	11387	1896	13	22370
	35	8	5	67	69	36	13	2	71	3	137	411
	36	1	4	29	53	20	21	3	32	4	69	236

Tw3 250m

	EFTs	PW	Cr(Fld)	Cr	CF	SG	Ca	GW	NF	Sh	B/U	Total
Hapludult	25	0	7	760	1378	1381	2131	38	6094	507	27	12323
	26	0	1	59	20	42	92	11	108	0	4	337
	27	0	0	38	13	14	36	9	25	0	4	139
	28	0	5	180	87	218	455	45	193	4	19	1206
	29	0	12	775	351	467	1261	150	1827	49	45	4937
	30	0	13	510	312	528	1698	120	1104	20	45	4350
	31	0	3	100	70	97	126	35	154	2	14	601
	32	0	8	680	355	989	2418	118	997	16	69	5650
	33	0	14	92	155	97	191	25	391	26	40	1031
	34	0	9	125	135	111	296	26	81	0	32	815
	35	0	5	41	24	17	37	7	17	0	7	155
	36	0	5	100	41	85	168	26	78	0	12	515
Dystrudept	25	0	0	175	1094	363	186	54	1314	385	0	3571
	26	0	0	0	0	0	0	0	0	0	0	0
	27	0	0	0	0	0	0	0	0	0	0	0
	28	0	0	0	0	0	0	0	0	0	0	0
	29	0	0	0	4	1	4	0	8	3	0	20
	30	0	0	0	1	0	1	0	0	0	0	2
	31	0	0	0	0	0	0	0	0	0	0	0
	32	0	0	0	0	0	0	0	1	1	0	2
	33	0	0	33	177	57	25	6	186	40	0	524
	34	0	0	0	0	0	0	0	0	0	0	0
	35	0	0	0	0	0	0	0	0	0	0	0
	36	0	0	0	0	0	0	0	0	0	0	0
Argiudoll	25	0	2	586	650	665	318	85	2625	245	33	5209
	26	0	9	83	32	25	10	63	58	0	8	288
	27	0	10	39	25	6	10	41	22	0	6	159
	28	0	1	108	43	62	66	48	70	1	10	409
	29	0	32	771	175	232	191	318	721	7	47	2494
	30	0	3	303	78	153	139	95	250	4	36	1061
	31	0	4	93	32	40	19	44	88	2	19	341
	32	0	5	351	122	162	135	137	198	0	43	1153
	33	1	39	114	120	63	27	131	217	14	46	772
	34	0	1	78	77	36	96	38	53	0	20	399
	35	0	1	17	19	11	3	16	11	0	9	87
	36	0	0	53	28	22	22	23	22	0	5	175
Humaquept	25	0	31	52	170	31	0	18	87	0	173	562
	26	0	17	3	20	0	0	4	11	0	26	81
	27	0	9	1	14	1	0	2	12	0	11	50
	28	0	9	6	39	2	0	1	9	0	42	108
	29	2	91	64	202	24	0	29	71	0	205	688
	30	2	22	33	162	14	0	12	31	0	163	439
	31	0	41	6	103	3	0	7	14	0	132	306

	32	1	27	27	104	7	0	16	8	0	93	283
	33	3	38	29	85	18	0	27	72	0	95	367
	34	4	13	16	120	2	0	10	17	0	434	616
	35	0	8	9	35	1	0	7	13	0	26	99
	36	0	10	6	53	1	0	4	9	0	44	127
Eutr.Udorthent	25	4	19	143	159	116	37	11	286	7	204	986
	26	1	0	3	17	5	0	0	8	0	23	57
	27	0	1	1	9	0	0	0	1	0	7	19
	28	0	15	29	114	1	0	1	11	0	112	283
	29	7	16	94	107	29	1	5	49	0	133	441
	30	6	33	184	259	65	3	21	67	0	268	906
	31	1	3	8	43	9	1	0	11	0	33	109
	32	7	26	169	249	36	5	25	66	0	309	892
	33	3	11	24	51	9	2	0	38	0	46	184
	34	13	66	85	347	34	0	8	85	0	605	1243
	35	2	2	10	35	4	0	6	5	0	53	117
	36	0	15	30	143	10	1	4	22	0	214	439
Albaqualf / Duraqualf	25	0	15	96	96	59	75	60	149	0	44	594
	26	0	10	51	39	22	4	23	26	0	20	195
	27	0	8	27	41	20	1	24	17	0	17	155
	28	0	39	183	312	139	46	106	57	0	136	1018
	29	0	61	221	254	156	94	153	161	0	126	1226
	30	1	40	485	357	366	142	215	166	0	200	1972
	31	0	21	81	129	68	17	65	33	0	61	475
	32	1	95	785	761	590	206	352	197	0	391	3378
	33	1	50	124	415	60	6	88	41	0	176	961
	34	4	74	254	700	88	54	118	64	0	290	1646
	35	2	24	104	129	24	0	52	11	0	69	415
	36	1	33	118	267	63	29	78	42	0	116	747
Argiudoll / E.Udorthent	25	2	1	1364	3741	3318	993	87	11580	1876	97	23059
	26	1	0	3	2	0	2	0	7	0	0	15
	27	0	0	0	1	1	0	0	0	0	0	2
	28	1	0	8	9	11	5	1	12	1	20	68
	29	1	5	183	106	146	77	1	500	35	70	1124
	30	4	4	65	53	45	20	4	129	5	58	387
	31	0	2	14	10	15	10	0	50	3	9	113
	32	1	7	44	26	25	12	4	78	2	58	257
	33	0	1	145	357	295	85	13	897	155	45	1993
	34	4	1	26	61	13	12	3	47	0	104	271
	35	0	0	7	2	3	2	1	4	1	11	31
	36	0	0	19	13	9	1	1	11	0	33	87

W3-1Km

	EFTs	PW	Cr(Fld)	Cr	CF	SG	Ca	GW	NF	Sh	B/U	Total
Hapludult	44	0	0	561	1171	1144	1436	0	5084	462	8	9866
	45	0	0	19	48	39	47	0	160	20	0	333
	46	0	4	812	547	537	1752	92	2805	92	27	6668
	47	0	0	266	139	154	261	69	407	11	11	1318
	48	0	28	999	460	1239	3280	236	1787	28	65	8122
	49	0	1	25	25	16	17	14	70	6	10	184
	50	0	31	617	328	794	1757	155	608	3	111	4404
	51	0	18	161	223	123	359	44	148	2	86	1164
	52	0	0	0	0	0	0	0	0	0	0	0
Dytrudept	44	0	0	183	1058	367	174	54	1310	341	0	3487
	45	0	0	18	154	38	24	5	130	45	0	414
	46	0	0	0	0	0	0	0	0	0	0	0
	47	0	0	1	31	3	4	0	26	17	0	82
	48	0	0	0	0	0	0	0	0	0	0	0
	49	0	0	6	18	9	8	0	27	20	0	88
	50	0	0	0	15	4	6	1	16	6	0	48
	51	0	0	0	0	0	0	0	0	0	0	0
	52	0	0	0	0	0	0	0	0	0	0	0
Argiudoll	44	0	0	418	598	563	208	6	2371	230	38	4432
	45	0	0	5	9	10	9	0	49	8	0	90
	46	0	41	1040	213	332	407	417	1069	21	66	3606
	47	1	10	355	126	153	66	147	295	5	45	1203
	48	0	7	457	194	271	152	244	249	1	47	1622
	49	0	10	87	86	40	20	114	137	6	31	531
	50	0	0	118	67	72	99	44	107	2	22	531
	51	0	39	124	109	37	75	67	59	0	34	544
	52	0	0	2	0	1	0	0	4	0	0	7
Humaquept	44	1	3	0	6	1	0	0	6	0	6	23
	45	0	0	0	0	0	0	0	0	0	0	0
	46	0	101	68	154	39	0	37	119	0	208	726
	47	0	44	27	190	12	0	13	47	0	228	561
	48	3	50	74	287	31	0	15	63	0	253	776
	49	1	24	2	29	1	0	1	10	0	30	98
	50	2	49	48	137	8	0	43	30	0	128	445
	51	15	59	34	359	14	0	28	85	0	783	1377
	52	10	4	0	19	0	0	0	0	0	24	57
E.Udorthent	44	0	3	29	64	44	23	3	104	2	39	311
	45	0	0	0	0	0	0	0	0	0	0	0
	46	3	23	36	31	14	0	1	16	0	44	168
	47	0	5	160	90	75	7	11	129	3	85	565
	48	16	65	244	383	72	8	42	130	0	450	1410
	49	0	0	2	14	13	0	0	21	1	7	58
	50	6	28	130	350	46	4	10	119	1	428	1122

	51	39	104	198	654	60	10	15	156	0	1163	2399
	52	38	13	8	31	6	0	0	5	0	89	190
Albaqualf / Duraqualf	44	0	1	3	4	4	10	1	32	0	2	57
	45	0	0	0	0	0	0	0	0	0	0	0
	46	0	34	114	100	56	36	117	135	0	36	628
	47	0	39	170	87	129	53	48	102	0	49	677
	48	0	103	766	645	644	316	328	340	0	401	3543
	49	1	28	52	89	6	0	36	37	0	39	288
	50	3	147	1148	1412	717	188	624	234	0	612	5085
	51	6	121	278	1165	99	71	181	85	0	513	2519
	52	0	0	0	0	0	0	0	0	0	0	0
Argiudoll / E.Udorthent	44	0	1	1301	3667	3186	927	78	11400	1836	51	22447
	45	0	1	107	174	203	52	10	514	87	9	1157
	46	0	0	195	155	211	121	8	688	71	14	1463
	47	1	3	81	85	90	29	7	220	17	92	625
	48	1	11	55	37	32	14	6	93	8	60	317
	49	0	0	23	76	71	22	1	171	41	3	408
	50	7	3	76	89	57	11	3	101	7	87	441
	51	7	2	45	105	39	48	6	161	15	206	634
	52	3	5	6	3	5	1	0	28	0	17	68

W3-250m

	EFTs	PW	Cr(Fld)	Cr	CF	SG	Ca	GW	NF	Sh	B/U	Total
Hapludult	45	0	3	470	1030	1005	1250	8	4280	398	12	8456
	46	0	0	17	46	46	65	1	173	19	0	367
	47	0	1	755	499	570	1391	100	2827	120	25	6288
	48	0	7	268	184	265	892	39	832	27	22	2536
	49	0	6	194	82	105	204	54	323	7	14	989
	50	0	21	687	413	792	2067	184	1320	28	60	5572
	51	0	18	132	138	124	164	44	164	7	54	845
	52	0	26	937	549	1139	2876	180	1150	18	131	7006
	53	0	0	0	0	0	0	0	0	0	0	0
Dytrudept	45	0	0	162	993	333	164	50	1182	332	0	3216
	46	0	0	33	155	52	24	6	166	34	0	470
	47	0	0	1	31	4	10	0	41	13	0	100
	48	0	0	0	1	0	1	0	2	0	0	4
	49	0	0	2	9	1	4	0	12	3	0	31
	50	0	0	0	1	0	1	0	0	1	0	3
	51	0	0	10	68	25	9	4	90	37	0	243
	52	0	0	0	18	6	3	0	16	9	0	52
	53	0	0	0	0	0	0	0	0	0	0	0
Argiudoll	45	0	0	322	568	545	204	15	2023	219	13	3909
	46	0	0	21	41	22	15	1	93	13	3	209
	47	0	38	742	180	216	221	354	969	23	39	2782
	48	0	2	153	45	64	69	70	167	2	27	599
	49	0	10	193	60	72	22	86	208	3	24	678

	50	0	4	541	133	227	188	152	391	4	41	1681
	51	1	48	159	137	57	36	174	183	5	57	857
	52	0	5	472	237	276	281	187	306	4	79	1847
	53	0	0	3	1	0	0	0	0	0	0	4
Humaquept	45	0	4	10	32	7	0	0	22	0	42	117
	46	0	0	2	3	0	0	1	0	0	4	10
	47	1	88	56	148	26	0	37	95	0	199	650
	48	0	20	19	73	12	0	6	24	0	71	225
	49	1	19	15	131	5	0	8	25	0	129	333
	50	3	40	71	253	30	0	12	54	0	240	703
	51	5	100	23	209	9	0	38	90	0	343	817
	52	8	51	57	297	17	0	35	49	0	604	1118
	53	14	12	0	35	0	0	0	1	0	28	90
E.Udorthent	45	0	6	80	87	78	30	10	206	7	97	601
	46	0	0	4	9	4	0	0	8	0	4	29
	47	3	13	39	52	22	4	1	48	0	74	256
	48	3	8	26	80	5	0	0	18	0	67	207
	49	4	6	60	67	23	2	3	50	0	89	304
	50	10	43	255	316	93	5	27	106	0	385	1240
	51	27	25	50	197	27	3	2	64	0	308	703
	52	35	112	284	759	76	8	39	169	0	1234	2716
	53	20	28	9	50	2	0	0	11	0	47	167
Albaqualf / Duraqualf	45	0	4	35	28	19	32	19	83	0	6	226
	46	0	1	2	4	0	1	3	0	0	3	14
	47	0	37	123	139	83	64	97	117	0	57	717
	48	0	21	168	98	131	47	95	70	0	63	693
	49	0	30	72	87	37	28	40	61	0	40	395
	50	0	55	577	534	459	201	260	230	0	288	2604
	51	3	127	319	895	128	26	195	93	0	386	2172
	52	7	197	1234	1715	798	275	625	310	0	807	5968
	53	0	1	1	2	0	0	1	1	0	2	8
Argiudoll / E.Udorthent	45	2	1	1098	3393	2927	837	72	10138	1674	47	20189
	46	0	0	118	320	251	64	11	788	128	25	1705
	47	1	1	326	269	367	170	3	1416	151	49	2753
	48	1	1	39	27	67	18	2	119	9	16	299
	49	1	1	62	42	41	33	3	177	7	38	405
	50	4	9	98	72	55	32	2	208	12	86	578
	51	0	1	54	143	124	39	15	327	84	83	870
	52	7	9	90	119	60	32	8	192	17	173	707
	53	3	3	4	6	2	0	3	11	0	22	54

A2. Maximum positive and maximum negative deviations from random distribution ($_{\max}(\pm)D_{ij|k}$), associated to the land-cover types in the *i*th EFT and the *k*th soil unit. These divergences are presented as a fraction of the total negative and positive divergences associated to the corresponding EFTs in the soil unit ($+\Delta_{ik}$ and $-\Delta_{ik}$).

Window 1

		Dystrudept				Hapludox				Eutr.Udorthent			
	EFTs	Positive		Negative		Positive		Negative		Positive		Negative	
W 250m	1	0.51	GW	0.63	NF	0.85	Ca	0.51	NF	0.44	Ca	0.61	NF
	2	0.49	Ca	0.81	NF	1.00	Ca	0.35	Cr	1.00	Sh	0.32	Ca
	3	0.60	Sh	0.75	Ca	0.96	Cr	0.88	Ca	0.66	SG	0.39	CF
	4	0.58	NF	0.76	Ca	0.52	NF	0.73	Ca	0.40	Ca	0.42	CF
	5	0.72	Sh	0.50	CF	0.39	Sh	0.66	Ca	0.54	GW	0.46	Ca
	6	0.40	Sh	0.65	NF	0.62	Sh	0.50	Cr	0.39	Cr	0.35	NF
	7	0.40	Sh	0.69	Ca	0.44	NF	0.57	Ca	0.58	GW	0.79	NF
	8	0.81	NF	0.55	Ca	0.42	NF	0.60	Ca	0.48	SG	0.49	Sh
	9	0.75	NF	0.62	Ca	0.50	NF	0.66	Ca	0.70	NF	0.46	Sh
	10	0.56	CF	0.63	Ca	0.52	NF	0.74	Ca	0.70	Cr	0.58	GW
	11	0.64	NF	0.62	Ca	0.50	NF	0.67	Ca	0.65	NF	0.41	Ca
	12	0.70	NF	0.63	Ca	0.45	NF	0.71	Ca	0.53	NF	0.62	Ca
	13	0.49	NF	0.59	Ca	0.45	CF	0.68	Ca	0.53	NF	0.35	Sh
	14	0.58	CF	0.82	Ca	0.60	NF	0.73	Ca	0.40	Cr	0.41	Ca
	15	0.57	NF	0.62	Ca	0.52	CF	0.68	Ca	0.63	SG	0.36	NF
	16	0.58	CF	0.67	Ca	0.61	CF	0.69	Ca	0.89	NF	0.44	GW
	17	0.70	Ca	0.62	NF	0.79	Ca	0.53	NF	0.50	GW	0.44	NF
	18	0.85	Ca	0.61	NF	1.00	Ca	0.39	NF	0.56	Ca	0.65	NF
	19	0.83	Ca	0.44	NF	1.00	Ca	0.39	NF	1.00	GW	0.41	NF
	20	0.84	Ca	0.57	NF	0.69	Cr	0.52	NF	0.34	Ca	0.67	NF
W 1Km	1	0.50	Sh	0.62	NF	0.36	NF	0.54	Ca	0.74	GW	0.58	NF
	2	0.85	Ca	0.70	NF	0.61	Sh	0.62	Cr	0.40	GW	0.57	NF
	3	0.37	Sh	0.80	Ca	0.58	Sh	0.98	Ca	0.50	Sh	0.38	SG
	4	0.42	Sh	0.80	Ca	0.78	NF	0.48	Cr	0.49	Sh	0.42	NF
	5	0.58	NF	0.67	Ca	0.44	NF	0.58	Ca	0.79	NF	0.40	Sh
	6	0.61	NF	0.80	Ca	0.62	NF	0.63	Ca	0.56	Ca	0.46	NF
	7	0.92	Ca	0.56	NF	0.47	Ca	0.77	Cr	--	--	--	--
	8	0.81	Ca	0.57	NF	0.95	Ca	0.41	NF	0.52	Sh	0.52	NF
	9	0.36	GW	0.55	NF	0.75	Ca	0.62	Cr	0.53	Ca	0.47	NF
	10	0.70	Cr	0.39	NF	0.92	Cr	0.47	NF	--	--	--	--
	11	0.98	Ca	0.44	NF	1.00	Ca	0.37	NF	--	--	--	--
	12	0.62	NF	0.70	Ca	0.35	NF	0.66	Ca	0.56	CF	0.48	GW
	13	0.65	NF	0.57	Ca	0.63	NF	0.60	Ca	0.57	CF	0.61	GW
	14	0.52	NF	0.62	Ca	0.52	NF	0.69	Ca	0.44	SG	0.47	Sh
	15	0.67	NF	0.63	Ca	0.38	NF	0.65	Ca	0.31	SG	0.44	CF
	16	0.70	NF	0.62	Ca	0.49	NF	0.71	Ca	0.57	NF	0.40	Ca
	17	0.85	NF	0.39	Ca	0.53	Sh	0.65	Ca	0.44	Cr	0.57	NF
	18	--	--	--	--	0.50	NF	0.60	Ca	--	--	--	--
	19	0.51	CF	0.68	Ca	0.47	CF	0.70	Ca	0.50	NF	0.54	Sh
	20	0.59	NF	0.63	Ca	0.49	NF	0.69	Ca	0.89	NF	0.31	Ca

	21	0.82	Ca	0.41	NF	0.92	Ca	0.52	NF	--	--	--	--
T 250m	1	0.57	NF	0.65	Ca	0.45	NF	0.70	Ca	0.72	NF	0.47	B/U
	2	0.48	NF	0.84	Ca	0.50	NF	0.66	Cr	0.35	Sh	0.57	B/U
	3	0.38	Ca	0.43	CF	0.76	Ca	0.36	NF	0.39	GW	0.29	B/U
	4	0.77	Ca	0.67	NF	1.00	Ca	0.40	NF	0.36	Ca	0.44	NF
	5	0.74	NF	0.77	Ca	0.50	NF	0.65	Ca	0.40	Sh	0.80	B/U
	6	0.61	Sh	0.84	Ca	0.39	NF	0.64	Ca	0.75	NF	0.30	B/U
	7	0.79	NF	0.74	Ca	0.52	NF	0.60	Ca	0.65	Ca	0.57	B/U
	8	0.53	Sh	0.47	NF	0.37	Sh	0.60	Cr	0.34	GW	0.43	B/U
	9	0.83	Cr	0.37	NF	1.00	Cr	0.37	NF	0.47	Cr	0.32	B/U
	10	0.56	Ca	0.40	NF	1.00	Cr	0.42	NF	0.85	B/U	0.43	NF
	11	0.47	Ca	0.60	NF	0.97	Ca	0.52	NF	0.64	Ca	0.46	NF
	12	0.83	Ca	0.61	NF	1.00	Ca	0.43	NF	0.64	GW	0.28	CF
T 1km	1	0.44	Sh	0.63	Ca	0.75	NF	0.56	Ca	0.34	GW	0.72	NF
	2	0.38	Sh	0.55	NF	0.62	Sh	0.75	Cr	0.39	Sh	0.39	NF
	3	1.00	Cr	0.33	SG	1.00	Cr	0.48	NF	0.50	GW	0.35	Ca
	4	0.69	NF	0.71	Ca	0.49	NF	0.67	Ca	0.49	Ca	0.48	GW
	5	0.65	NF	0.79	Ca	0.45	NF	0.64	Ca	0.47	Cr	0.45	GW
	6	0.63	NF	0.72	Ca	0.49	NF	0.64	Ca	0.45	Ca	0.31	Cr
	7	0.37	Sh	0.74	Ca	0.42	NF	0.58	Ca	0.75	NF	0.39	Ca
	8	--	--	--	--	0.64	NF	0.72	Ca	--	--	--	--
	9	0.61	NF	0.67	Ca	0.55	NF	0.71	Ca	0.72	NF	0.31	GW
	10	0.56	CF	0.62	Ca	0.47	NF	0.69	Ca	0.76	NF	0.38	Sh
	11	0.82	Ca	0.59	NF	1.00	Ca	0.37	Cr	0.69	GW	0.40	NF
	12	0.64	Ca	0.39	NF	0.58	Ca	0.45	NF	--	--	--	--

		Argiudoll / E.Udorthent				D.Udorthent / Humaquept			
	EFTs	Positive		Negative		Positive		Negative	
W 250m	1	0.47	SG	0.65	NF	1.00	NF	0.28	Ca
	2	0.96	Ca	0.55	NF	--	--	--	--
	3	0.53	Ca	0.59	NF	0.56	Ca	0.34	NF
	4	0.61	Ca	0.76	NF	0.62	CF	0.65	NF
	5	0.68	Ca	0.68	NF	0.50	Ca	0.62	Cr
	6	0.76	Ca	0.60	NF	1.00	Sh	0.48	NF
	7	0.68	Ca	0.48	NF	0.96	Ca	0.41	NF
	8	0.71	Ca	0.79	NF	0.66	CF	0.52	NF
	9	0.71	Ca	0.48	NF	0.62	Sh	0.63	CF
	10	0.34	Cr	0.55	NF	0.63	Ca	0.51	NF
	11	0.50	NF	0.74	CF	0.59	Cr	0.73	NF
	12	0.50	NF	0.68	Ca	0.89	NF	0.65	Ca
	13	0.83	NF	0.75	Ca	0.46	SG	0.71	Ca
	14	0.54	CF	0.42	SG	0.42	Ca	0.48	SG
	15	0.37	CF	0.41	Cr	0.52	Cr	0.33	Ca
	16	0.51	CF	0.65	Ca	0.78	CF	0.57	Ca
	17	0.28	Ca	0.47	NF	1.00	Sh	0.48	NF
	18	0.56	Ca	0.81	NF	0.77	Ca	0.58	NF
	19	--	--	--	--	--	--	--	--
	20	0.41	Ca	0.32	NF	--	--	--	--

W 1Km	1	0.73	Ca	0.35	SG	--	--	--	--
	2	0.64	SG	0.31	CF	--	--	--	--
	3	1.00	Ca	0.32	CF	--	--	--	--
	4	0.56	CF	0.52	Sh	1.00	Ca	0.52	NF
	5	0.51	Ca	0.72	NF	--	--	--	--
	6	0.62	Sh	0.37	SG	0.54	SG	0.51	Sh
	7	0.62	Ca	0.69	NF	--	--	--	--
	8	--	--	--	--	--	--	--	--
	9	--	--	--	--	--	--	--	--
	10	1.00	Ca	0.30	SG	--	--	--	--
	11	--	--	--	--	--	--	--	--
	12	0.47	Sh	0.46	NF	0.79	Ca	0.29	CF
	13	0.52	Ca	0.97	NF	0.80	Sh	0.31	NF
	14	0.58	Ca	0.72	NF	0.54	NF	0.53	Sh
	15	0.61	Ca	0.74	NF	0.33	NF	0.56	SG
	16	0.50	NF	0.30	Sh	0.63	SG	0.49	Ca
	17	0.61	CF	0.65	NF	0.62	NF	0.35	Cr
	18	0.51	SG	0.40	Ca	--	--	--	--
	19	0.73	NF	0.44	Ca	0.67	Cr	0.44	Ca
	20	0.55	NF	0.63	Ca	0.93	CF	0.79	Ca
	21	--	--	--	--	--	--	--	--
T 250m	1	0.71	NF	0.68	Ca	0.51	NF	0.83	Ca
	2	0.67	Ca	0.42	Sh	--	--	--	--
	3	0.40	Ca	0.87	NF	--	--	--	--
	4	0.59	Ca	0.80	NF	1.00	Ca	0.52	NF
	5	0.64	Ca	0.63	NF	0.87	Ca	0.62	NF
	6	0.77	Ca	0.73	NF	1.00	Ca	0.52	NF
	7	0.68	Ca	0.63	NF	0.47	Ca	0.43	Cr
	8	0.63	Ca	0.70	NF	1.00	Ca	0.35	NF
	9	0.53	CF	0.60	NF	--	--	--	--
	10	0.38	B/U	0.41	Sh	--	--	--	--
	11	0.39	Sh	0.59	NF	--	--	--	--
	12	0.87	Ca	0.52	SG	--	--	--	--
T 1km	1	0.89	NF	0.42	Sh	0.66	Ca	0.40	SG
	2	0.71	Ca	0.70	NF	--	--	--	--
	3	0.48	Ca	0.51	NF	--	--	--	--
	4	0.53	Ca	0.51	NF	0.58	Ca	0.50	Cr
	5	0.75	Ca	0.63	NF	--	--	--	--
	6	0.45	Sh	0.63	NF	0.63	Sh	0.44	Cr
	7	0.71	Ca	0.68	NF	--	--	--	--
	8	0.66	Sh	0.53	NF	--	--	--	--
	9	0.42	Cr	0.32	CF	0.73	Cr	0.33	SG
	10	0.57	NF	0.59	Ca	0.43	CF	0.69	Ca
	11	0.45	GW	0.30	CF	--	--	--	--
	12	0.65	Ca	0.46	NF	--	--	--	--

Window 2

		Dystrudept				Argiudoll				E.Udorthent				Argiudoll / E.Udorthent			
	EFTs	Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative	
W 250m	1	0.471	Ca	0.513	NF	--	--	--	--	0.347	GW	0.749	NF	1	GW	0.431	NF
	2	0.523	Ca	0.539	NF	--	--	--	--	0.465	GW	0.832	NF	1	NF	0.355	CF
	3	0.637	Ca	0.468	CF	1	Cr	0.565	NF	0.49	GW	0.682	NF	--	--	--	--
	4	0.459	GW	0.544	CF	--	--	--	--	0.822	Ca	0.467	Sh	0.8	GW	0.644	NF
	5	0.352	Sh	0.554	CF	--	--	--	--	0.324	SG	0.752	NF	0.6	GW	0.364	NF
	6	0.522	GW	0.589	CF	--	--	--	--	0.949	Ca	0.533	Sh	0.5	Sh	0.563	NF
	7	0.637	CF	0.419	Ca	0.827	CF	0.598	Cr	1	CF	0.436	Ca	0.8	CF	0.502	Sh
	8	0.591	NF	0.421	Ca	0.534	CF	0.719	NF	0.573	NF	0.317	Sh	0.9	NF	0.676	CF
	9	0.72	Ca	0.511	NF	--	--	--	--	0.525	CF	0.468	SG	--	--	--	--
	10	0.452	GW	0.72	CF	--	--	--	--	0.536	Sh	0.388	SG	0.8	GW	0.604	NF
	11	0.534	Ca	0.776	CF	--	--	--	--	0.742	NF	0.539	Ca	0.8	GW	0.76	NF
	12	0.365	GW	0.662	CF	--	--	--	--	0.561	NF	0.52	GW	0.6	Sh	0.351	SG
	13	0.576	NF	0.488	Ca	1	Cr	0.321	CF	0.945	NF	0.487	Ca	0.6	Sh	0.481	NF
	14	0.988	NF	0.407	Ca	0.953	NF	0.437	CF	0.982	NF	0.456	GW	0.5	Ca	0.64	SG
	15	0.897	CF	0.37	Ca	0.787	Sh	0.737	CF	0.417	Ca	0.402	GW	0.7	CF	0.746	NF
	16	0.61	CF	0.434	Ca	0.67	SG	0.571	NF	0.711	CF	0.493	Ca	0.6	NF	0.432	CF
	17	0.744	CF	0.426	Ca	0.757	Sh	0.534	NF	0.591	Sh	0.481	NF	0.4	Ca	0.453	CF
	18	0.521	CF	0.417	Ca	0.949	NF	0.712	CF	0.627	CF	0.488	Ca	0.4	NF	0.431	CF
	19	0.509	CF	0.407	Ca	0.839	NF	0.493	CF	0.381	Sh	0.535	Ca	0.4	Sh	0.687	CF
	20	0.546	NF	0.413	Ca	0.597	NF	0.464	CF	0.798	CF	0.386	GW	0.4	Cr	0.701	CF
	21	0.674	CF	0.377	Ca	0.45	SG	0.716	CF	0.665	CF	0.357	SG	0.6	Cr	0.464	SG
	22	0.469	NF	0.48	Ca	0.61	Cr	0.542	CF	0.732	NF	0.701	Ca	0.5	Sh	0.433	SG
	23	0.538	Ca	0.559	NF	--	--	--	--	0.615	Ca	0.766	NF	--	--	--	--
	24	0.526	Ca	0.442	NF	--	--	--	--	0.495	SG	0.525	NF	--	--	--	--
W 1Km	1	0.599	Ca	0.529	NF	--	--	--	--	--	--	--	--	--	--	--	--
	2	0.528	Ca	0.512	CF	--	--	--	--	0.515	GW	0.404	CF	--	--	--	--
	3	0.823	GW	0.398	NF	--	--	--	--	0.785	Sh	0.408	NF	--	--	--	--
	4	0.396	GW	0.708	CF	--	--	--	--	0.722	NF	0.385	Sh	1	GW	0.431	NF
	5	0.601	Sh	0.565	CF	--	--	--	--	0.737	NF	0.506	Ca	0.5	GW	0.641	NF
	6	0.725	GW	0.463	CF	--	--	--	--	--	--	--	--	0.8	GW	0.616	NF
	7	0.42	NF	0.62	Ca	--	--	--	--	0.447	Sh	0.729	Ca	0.5	Sh	0.629	NF
	8	0.523	Ca	0.542	CF	--	--	--	--	0.389	GW	0.757	NF	--	--	--	--
	9	0.494	Ca	0.555	NF	--	--	--	--	0.554	GW	0.861	NF	--	--	--	--
	10	0.566	Ca	0.689	CF	--	--	--	--	0.508	Ca	0.42	Sh	--	--	--	--
	11	0.446	Sh	0.535	CF	--	--	--	--	0.517	SG	0.344	CF	--	--	--	--
	12	0.49	NF	0.38	Ca	0.44	Sh	0.738	Cr	--	--	--	--	0.8	NF	0.457	Sh
	13	0.668	NF	0.408	Ca	0.495	CF	0.519	Cr	--	--	--	--	0.5	CF	0.398	Sh
	14	0.603	NF	0.466	Ca	0.91	CF	0.479	NF	--	--	--	--	0.4	NF	0.413	Sh
	15	0.63	CF	0.398	Ca	0.706	CF	0.722	NF	0.647	CF	0.404	Ca	0.7	NF	0.42	Ca
	16	0.59	CF	0.435	Ca	0.472	NF	0.501	CF	--	--	--	--	0.7	CF	0.578	NF
	17	0.676	CF	0.428	Ca	0.588	SG	0.838	NF	--	--	--	--	0.3	SG	0.772	CF
	18	0.674	CF	0.504	Ca	0.536	NF	0.436	CF	1	Sh	0.358	Ca	0.4	SG	0.732	NF

	19	0.64	CF	0.416	Ca	0.774	NF	0.523	CF	0.806	CF	0.347	Ca	0.6	NF	0.464	CF
	20	0.671	CF	0.405	Ca	1	Cr	0.32	NF	0.639	NF	0.318	Ca	0.6	Cr	0.697	SG
	21	0.636	CF	0.427	Ca	0.984	NF	0.49	CF	0.658	CF	0.337	NF	0.4	Sh	0.604	NF
	22	0.641	NF	0.521	Ca	--	--	--	--	0.565	Sh	0.561	NF	0.5	GW	0.599	NF
T 250m	1	0.586	CF	0.421	Ca	0.476	CF	0.723	Cr	0.782	CF	0.442	Ca	0.6	NF	0.364	Sh
	2	0.691	GW	0.668	CF	1	NF	0.363	CF	0.701	NF	0.305	GW	0.6	Sh	0.713	NF
	3	0.408	Ca	0.679	CF	--	--	--	--	1	NF	0.347	Sh	0.8	GW	0.657	NF
	4	0.392	Ca	0.542	CF	--	--	--	--	0.519	NF	0.428	CF	0.7	GW	0.53	NF
	5	0.846	NF	0.52	Ca	0.939	NF	0.478	CF	0.64	NF	0.378	Ca	0.4	Ca	0.692	NF
	6	0.59	NF	0.454	Ca	--	--	--	--	0.935	NF	0.489	SG	0.4	Sh	0.572	NF
	7	0.767	NF	0.39	GW	1	Cr	0.355	NF	1	NF	0.25	Sh	0.6	Sh	0.538	CF
	8	0.496	Sh	0.468	CF	1	Cr	0.469	NF	0.571	NF	0.639	Ca	0.5	Sh	0.325	SG
	9	0.705	CF	0.44	Ca	0.659	SG	0.77	NF	0.758	CF	0.493	Sh	0.5	Ca	0.389	Cr
	10	0.376	Sh	0.605	NF	--	--	--	--	0.702	GW	0.453	NF	--	--	--	--
	11	0.412	Ca	0.551	CF	--	--	--	--	0.809	NF	0.289	GW	--	--	--	--
	12	0.533	Ca	0.516	CF	--	--	--	--	0.275	GW	0.852	NF	0.8	B/U	0.6	NF
T 1Km	1	0.373	GW	0.722	CF	--	--	--	--	0.397	Sh	0.394	Ca	0.5	GW	0.641	NF
	2	0.4	GW	0.525	CF	--	--	--	--	0.78	NF	0.435	Ca	0.7	GW	0.598	NF
	3	0.766	Ca	0.4	SG	--	--	--	--	0.955	GW	0.404	NF	0.7	GW	0.773	NF
	4	0.52	NF	0.491	Ca	1	NF	0.363	CF	0.655	CF	0.445	GW	0.5	GW	0.758	NF
	5	0.604	CF	0.668	Ca	--	--	--	--	--	--	--	--	0.4	Sh	0.601	NF
	6	0.738	CF	0.344	Ca	--	--	--	--	0.597	Sh	0.537	NF	0.8	GW	0.484	NF
	7	0.597	CF	0.601	Ca	--	--	--	--	--	--	--	--	0.8	Sh	0.508	NF
	8	0.649	CF	0.323	Ca	0.913	CF	0.755	NF	--	--	--	--	0.9	SG	0.424	NF
	9	0.55	CF	0.57	Ca	0.746	Cr	0.477	CF	--	--	--	--	0.5	Sh	0.516	NF
	10	0.552	CF	0.432	Ca	0.372	SG	0.674	CF	0.578	CF	0.337	Ca	0.7	NF	0.483	Sh
	11	0.539	Ca	0.566	CF	--	--	--	--	0.462	Ca	0.489	CF	--	--	--	--
	12	0.33	GW	0.521	NF	--	--	--	--	0.61	Sh	0.356	GW	--	--	--	--

Window 3

		Hapludult				Dystrudept				Argiudoll				Humaquept			
	EFTs	Positive		Negative		Positive		Negative		Positive		Negative		Positive		Negative	
W 250m	1	0.736	NF	0.595	Ca	0.381	SG	0.413	Ca	0.657	NF	0.477	Cr	0.6	NF	0.317	B/U
	2	0.657	NF	0.525	Ca	0.415	CF	0.661	Sh	0.443	NF	0.476	Cr	0.6	Cr	0.415	NF
	3	0.896	NF	0.487	Ca	0.406	Ca	0.53	SG	0.53	Cr	0.419	CF	0.3	NF	0.596	B/U
	4	0.997	Ca	0.293	SG	0.596	Ca	0.314	Sh	0.349	Cr	0.484	NF	0.3	CF	0.862	B/U
	5	0.671	Cr	0.544	Ca	0.688	Ca	0.628	SG	0.55	Cr	0.356	Ca	1	CF	0.245	Cr(Fld)
	6	0.663	Ca	0.772	NF	0.526	Ca	0.687	NF	0.67	Cr	0.66	NF	0.6	CF	0.539	B/U
	7	0.291	CF	0.614	NF	0.88	Sh	0.548	CF	0.461	GW	0.505	NF	0.5	Cr(Fld)	0.406	CF
	8	0.627	Ca	0.857	NF	0.557	Sh	0.474	NF	0.34	Ca	0.876	NF	1	B/U	0.34	NF
	9	--	--	--	--	--	--	--	--	0.797	Cr	0.507	NF	0.5	PW	0.328	B/U
W 1Km	1	0.758	NF	0.59	Ca	0.611	NF	0.417	CF	0.751	NF	0.448	Cr	0.6	NF	0.54	B/U
	2	0.592	NF	0.599	Ca	0.861	CF	0.724	NF	0.701	NF	0.535	Cr	--	--	--	--
	3	0.845	NF	0.512	SG	--	--	--	--	0.55	Cr	0.357	CF	0.4	NF	0.585	B/U

	4	0.666	Cr	0.567	Ca	0.602	Sh	0.383	SG	0.576	Cr	0.657	NF	1	CF	0.295	Cr
	5	0.706	Ca	0.703	NF	--	--	--	--	0.342	Cr	0.883	NF	0.6	CF	0.654	B/U
	6	0.254	GW	0.825	Ca	0.687	Sh	0.587	CF	0.578	GW	0.382	NF	0.9	Cr(Fld)	0.558	B/U
	7	0.498	Ca	0.852	NF	0.709	Ca	0.493	Cr	0.61	Ca	0.844	NF	0.4	GW	0.787	B/U
	8	0.389	CF	0.851	NF	--	--	--	--	0.288	CF	0.768	NF	1	B/U	0.241	Cr(Fld)
	9									0.686	NF	0.339	CF	0.8	PW	0.398	NF
T 250m	1	0.781	NF	0.55	Ca	0.628	Sh	0.588	CF	0.766	NF	0.457	Cr	0.5	NF	0.679	B/U
	2	0.808	Cr	0.39	CF	--	--	--	--	0.554	GW	0.588	NF	0.7	Cr(Fld)	0.373	B/U
	3	0.714	Cr	0.714	NF	--	--	--	--	0.533	GW	0.63	NF	0.6	NF	0.688	B/U
	4	0.45	Ca	0.838	NF	--	--	--	--	0.382	Ca	0.845	NF	1	CF	0.421	GW
	5	0.576	Cr	0.371	SG	0.65	Ca	0.484	CF	0.676	Cr	0.373	NF	0.5	Cr(Fld)	0.959	B/U
	6	0.857	Ca	0.697	NF	0.702	Ca	0.574	NF	0.458	Cr	0.64	NF	0.8	CF	0.409	Cr(Fld)
	7	0.337	Cr	0.513	NF	--	--	--	--	0.443	Cr	0.589	NF	0.4	Cr(Fld)	0.372	NF
	8	0.696	Ca	0.783	NF	0.748	Sh	0.585	CF	0.474	Cr	0.845	NF	0.5	CF	0.518	NF
	9	0.409	CF	0.646	Ca	0.595	CF	0.591	Sh	0.412	GW	0.305	NF	0.5	NF	0.663	B/U
	10	0.321	Ca	0.927	NF	--	--	--	--	0.566	Ca	0.761	NF	1	B/U	0.319	CF
	11	0.504	Cr	0.758	NF	--	--	--	--	0.355	CF	0.729	NF	0.4	CF	0.833	B/U
	12	0.383	Cr	0.86	NF	--	--	--	--	0.384	Cr	0.879	NF	1	CF	0.342	B/U
T 1Km	1	0.424	GW	0.515	NF	--	--	--	--	0.702	GW	0.543	NF	0.7	Cr(Fld)	0.348	CF
	2	0.48	Ca	0.804	NF	--	--	--	--	0.315	GW	0.901	NF	0.4	Cr(Fld)	0.725	B/U
	3	0.371	CF	0.64	NF	1	CF	0.484	NF	0.529	GW	0.426	NF	1	B/U	0.378	CF
	4	0.502	Cr	0.4	Ca	--	--	--	--	0.932	Cr	0.313	CF	0.4	CF	0.51	B/U
	5	0.949	Ca	0.549	SG	0.837	NF	0.53	SG	0.531	Cr	0.434	NF	0.4	NF	0.436	CF
	6	0.473	NF	0.756	Ca	--	--	--	--	0.539	GW	0.277	NF	0.5	B/U	0.399	Cr
	7	0.564	Ca	0.746	NF	--	--	--	--	0.416	Cr	0.837	NF	0.6	CF	0.506	NF
	8	0.794	NF	0.408	Cr	0.785	CF	0.36	SG	0.645	NF	0.54	Cr	0.9	CF	0.501	B/U
	9	0.993	NF	0.402	Ca	1	NF	0.489	CF	0.375	NF	0.541	CF	0.8	Cr(Fld)	0.556	CF
	10	0.732	NF	0.64	Ca	0.398	SG	0.864	CF	0.682	NF	0.454	Cr	--	--	--	--
	11	0.352	Ca	0.93	NF	--	--	--	--	0.576	Cr	0.822	NF	0.9	CF	0.55	B/U
	12	0.331	CF	0.824	NF	--	--	--	--	0.37	Ca	0.761	NF	0.9	CF	0.424	Cr

		E.Udorthent				Albaqualf / Duraqualf				Argiudoll / E.Udorthent			
	EFTs	Positive		Negative		Positive		Negative		Positive		Negative	
W 250m	1	0.632	NF	0.566	B/U	0.766	NF	0.393	CF	0.459	NF	0.471	B/U
	2	0.537	NF	0.749	B/U	0.422	GW	0.497	SG	0.765	CF	0.625	NF
	3	0.511	NF	0.531	B/U	0.516	NF	0.469	CF	0.519	Cr	0.641	CF
	4	1	CF	0.369	B/U	0.336	SG	0.743	CF	0.41	SG	0.433	NF
	5	0.465	Cr	0.534	B/U	0.58	NF	0.392	CF	0.418	Cr	0.288	Sh
	6	0.713	Cr	0.562	B/U	0.434	SG	0.634	CF	0.493	B/U	0.479	NF
	7	0.615	B/U	0.532	Cr	0.662	CF	0.337	SG	0.65	B/U	0.939	NF
	8	0.783	B/U	0.439	NF	0.403	CF	0.69	NF	0.7	B/U	0.665	NF
	9	0.474	Cr(Fld)	0.327	B/U	0.433	B/U	0.463	SG	0.7	B/U	0.508	NF
W 1Km	1	0.586	NF	0.637	B/U	0.798	NF	0.334	CF	0.673	NF	0.517	B/U
	2	--	--	--	--	--	--	--	--	0.543	SG	0.653	NF
	3	0.458	Cr(Fld)	0.506	B/U	0.573	NF	0.47	CF	0.605	Cr	0.498	CF

	4	0.419	Cr	0.6	B/U	0.319	NF	0.615	CF	0.623	B/U	0.65	NF
	5	0.548	Cr	0.648	B/U	0.41	SG	0.716	CF	0.521	B/U	0.59	NF
	6	0.575	NF	0.567	B/U	0.338	Cr(Fld)	0.608	SG	0.348	SG	0.704	NF
	7	0.825	CF	0.219	Cr	0.451	Cr	0.473	NF	0.511	B/U	0.738	NF
	8	0.868	B/U	0.358	Cr	0.684	CF	0.326	SG	0.841	B/U	0.637	NF
	9	0.59	PW	0.311	CF	--	--	--	--	0.629	B/U	0.315	CF
T 250m	1	0.629	NF	0.525	B/U	0.705	NF	0.451	CF	0.616	NF	0.535	B/U
	2	0.343	B/U	0.582	Cr	0.425	Cr	0.493	CF	0.459	Cr	0.494	SG
	3	0.868	CF	0.361	Cr	0.507	GW	0.465	Ca	0.513	SG	0.695	NF
	4	0.693	CF	0.394	NF	0.709	CF	0.422	NF	0.691	B/U	0.776	NF
	5	0.809	Cr	0.556	B/U	0.494	NF	0.588	CF	0.567	Cr	0.394	CF
	6	0.619	Cr	0.545	B/U	0.41	SG	0.678	CF	0.499	B/U	0.578	NF
	7	0.815	CF	0.419	Cr	0.606	GW	0.51	Cr	0.345	B/U	0.402	CF
	8	0.694	Cr	0.538	NF	0.514	SG	0.552	CF	0.587	B/U	0.516	NF
	9	0.692	NF	0.778	B/U	0.693	CF	0.302	Cr	0.503	CF	0.932	NF
	10	0.824	B/U	0.427	Cr	0.726	CF	0.364	SG	0.758	B/U	0.648	NF
	11	0.569	B/U	0.41	NF	0.304	Cr	0.413	SG	0.621	B/U	0.659	NF
	12	0.706	B/U	0.364	Cr	0.708	CF	0.382	SG	0.697	B/U	0.694	NF
T 1Km	1	1	CF	0.418	B/U	0.623	Cr(Fld)	0.316	CF	--	--	--	--
	2	0.923	CF	0.343	NF	0.364	SG	0.323	Ca	0.493	NF	0.455	Sh
	3	0.917	B/U	0.324	Cr	0.649	CF	0.323	SG	0.673	B/U	0.791	NF
	4	0.49	Cr	0.577	B/U	0.547	NF	0.5	CF	0.755	Cr	0.396	CF
	5	0.544	Cr	0.6	B/U	0.511	NF	0.626	CF	0.478	Cr	0.604	NF
	6	0.588	SG	0.4	Cr	0.487	Ca	0.618	CF	0.452	Ca	0.639	SG
	7	0.708	Cr	0.527	CF	0.608	SG	0.601	CF	0.591	B/U	0.552	NF
	8	0.802	NF	0.449	B/U	0.704	NF	0.313	Cr	0.401	Ca	0.33	NF
	9	--	--	--	--	1	NF	0.404	CF	0.555	Ca	0.504	CF
	10	0.339	Ca	0.599	B/U	0.785	NF	0.328	CF	0.594	NF	0.46	B/U
	11	0.616	CF	0.387	NF	0.324	CF	0.418	SG	0.702	B/U	0.698	NF
	12	0.525	CF	0.425	Cr	0.637	CF	0.382	SG	0.588	B/U	0.752	NF

CONSIDERAÇÕES GERAIS

A heterogeneidade funcional é tanto um controle da resposta dos ecossistemas ao seu ambiente, quanto é também uma manifestação dessa resposta. Portanto, as conseqüências da heterogeneidade podem se retroalimentar na estrutura e no funcionamento dos sistemas ecológicos, produzindo mudanças complexas tanto nos padrões funcionais como de distribuição espacial dos ecossistemas perante os processos de mudança ambiental em curso. Nesta tese apresentamos uma nova linha de desenvolvimento teórico e metodológico, baseado no conceito de Tipos Funcionais de Ecossistemas, que visa contribuir para o estudo da heterogeneidade funcional. Postulados referentes à natureza dinâmica do funcionamento, encapsulado em pixels de imagens multiespectrais, e à existência de áreas funcionalmente homogêneas são de máxima importância. A novidade desta abordagem está também ligada às inovações metodológicas e analíticas que permitem tratar eficientemente os efeitos de incertezas ecológicas e de erros derivados do processo de sensoriamento remoto, no momento de se relacionar funcionamento e estrutura dos ecossistemas, assim como também à influência que os fatores de hábitat exercem sobre esse relacionamento. O conceito introduzido, poderia se enquadrar no contexto da dinâmica hierárquica de mosaicos e assim oferecer condições favoráveis para fazer *scaling* no espaço e no tempo, interligando processos que ocorrem no nível de organização dos ecossistemas e das paisagens.

Para tratar o problema geral da heterogeneidade espacial do funcionamento ecossistêmico escolhemos como área de estudo a região norte do Rio Grande do Sul. A região se caracteriza pela ocorrência de mosaicos naturais de vegetação campestre e florestal, assim como por uma dinâmica muito importante de mudança nos usos da terra. A plena compreensão do significado ecológico das unidades funcionais demandou assim uma exploração inicial da distribuição característica da vegetação e dos ecossistemas no espaço definido pelas variáveis ambientais. Observamos que existe uma associação mais ou menos nítida entre os dois tipos fisionômicos dominantes da vegetação, unidades de solo e domínios geomorfológicos específicos, na escala regional. No entanto, dentro de domínios de solos e de relevo específicos, a ocorrência de um ou outro tipo de vegetação não segue um padrão tão claro, podendo estar relacionada com a dinâmica histórica de uso da terra, com fenômenos locais de erosão e/ou acresção do terreno, e/ou com a dinâmica de distúrbios (fogo e pastejo). É assim que a interpretação dos padrões de associação espacial demanda desenvolvimentos metodológicos que possibilitem fazer '*down-scaling*' desde a escala regional, na qual os processos formadores de relevo e de solos dominam a diferenciação espacial de variáveis ecológicas, até a escala local, na qual fatores culturais, biológicos e relacionados com regimes de distúrbio adquirem maior importância. A maneira mais promissora de realizar essa tarefa é através da exploração da heterogeneidade funcional dos grandes tipos de vegetação, visando estabelecer como os diferentes fatores ambientais influenciam diferencialmente o funcionamento da vegetação e contribuem assim para segregar seus tipos no espaço.

O método de identificação de Tipos funcionais de ecossistemas que propomos emprega séries temporais de imagens multi-espectrais de resolução moderada (MODIS), com cobertura temporal de um ciclo anual. Neste trabalho as imagens escolhidas provinham dos datasets MOD13 (NDVI) e MOD15 (LAI e FPAR), e o tempo considerado foi o intervalo entre 16-dezembro 2001 até 31-dezembro de 2002. As imagens foram reamostradas para cobrir a área de estudo e reprojetadas conforme ao Sistema Global Geodético 84 (WGS84). Cada série foi dividida por estações, as imagens com valores médios de variáveis funcionais (NDVI, LAI ou FPAR) anormalmente baixos foram eliminadas e descritores de funcionamento foram calculados para cada estação. O critério para identificar TFEs foi o de trajetórias similares de descritores sazonais de funcionamento. Assim, os descritores sazonais foram empregados para produzir mapas sazonais usando a rotina não supervisionada de classificação CLUSTER. Posteriormente a sobreposição de mapas sazonais consecutivos permitiu o reconhecimento de grupos de pixels com idêntica seqüência de tipos sazonais. Quando esses grupos ocuparam pelo menos 1 por cento da área de estudo foram considerados significativos e usados para criar as assinaturas espectrais dos TFEs. Os pixels dos outros grupos foram realocados aos grupos significativos por meio de uma rotina supervisionada de classificação Maximum Likehood.

Devido a diversas fontes de incerteza, como a qualidade variável dos dados MODIS ou a relativamente curta série temporal sob análise, um grau indeterminado de erro era esperado na alocação dos pixels aos TFEs. Portanto foi preciso avaliar primeiro o produto das classificações funcionais. Uma maneira compreensiva de fazer tal avaliação foi a de analisar a associação espacial dos TFEs com tipos reconhecíveis de vegetação e unidades ambientais, assumindo que a heterogeneidade funcional é basicamente uma propriedade emergente da distribuição das feições adaptativas da vegetação em interação com a distribuição dos controles do ambiente biofísico. Representamos sucintamente a distribuição espacial das feições adaptativas da vegetação em um mapa de tipos fisionômicos / usos da terra, enquanto a distribuição espacial de controles biofísicos foi representada pelo mapa de solos correspondente. Postulamos que, quanto mais significativa e numericamente robusta a interação espacial encontrada, mais confiável a classificação funcional obtida.

Nossos resultados mostraram que: 1- Séries temporais MODIS-Land MOD13 e MOD15, com cobertura temporal de um ano, são apropriadas para classificar Tipos Funcionais de Ecossistemas (TFEs). O método classificatório, baseado na identificação de trajetórias, permite que a visão resultante da heterogeneidade funcional no espaço não seja excessivamente sensível às variações ao acaso que dominam a dinâmica dos fatores vegetacionais e climáticos no curto prazo. Porém, 2- a forma da interação entre a heterogeneidade funcional e a heterogeneidade estrutural da vegetação (associação espacial entre TFEs e tipos fisionômicos) é altamente dependente do contexto ambiental. Assim, tendências mais interpretáveis de associação espacial são observadas quando a sua relação recíproca é analisada num espaço definido por variáveis ambientais relevantes. No entanto, 3- a heterogeneidade espacial refletida pelos TFEs é altamente sensível à definição de funcionamento, decorrente da escolha de parâmetros MODIS e de seus descritores sazonais, assim como à variação de parâmetros de escala espacial que definem a resolução, a localização e a extensão espacial da informação funcional de base. E 4- observamos que o efeito da mudança dos parâmetros de escala espacial, na identificação dos padrões espaciais de heterogeneidade funcional, afeta a estrutura da associação espacial dos TFEs com os tipos fisionômicos e as unidades de solo. Porém, o efeito desses parâmetros não é independente da heterogeneidade ambiental contida na área de estudo. Assim, para obter uma visão mais precisa e detalhada da relação entre estrutura e funcionamento, além de empregar dados de maior resolução e cobertura espacial menor é preciso restringir a área de estudo segundo variáveis ambientais relevantes.

A sensibilidade dos TFEs à definição de funcionamento possibilita o uso do conceito para explorar o caráter multidimensional deste atributo dos ecossistemas. No entanto, a sensibilidade da classificação funcional aos parâmetros de escala espacial oferece vantagens importantes para aplicar o conceito aqui desenvolvido no contexto dos programas de pesquisa ecológica em multiplas escalas.