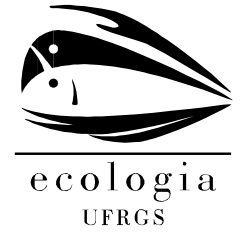**Universidade Federal do Rio Grande do Sul**

Instituto de Biociências

Programa de Pós-Graduação em Ecologia

Tese de Doutorado

Padrões de diversidade em comunidades de aves relacionados a variáveis de habitat em campos temperados do sudeste da América do Sul

Rafael Antunes Dias

Porto Alegre, Abril de 2013

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Padrões de diversidade em comunidades de aves relacionados às variáveis de habitat em campos temperados do sudeste da América do Sul

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À minha esposa Vânia.

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Life is like a box of chocolates,

you never know what you're gonna get.

Mrs. Gump

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RESUMO

Indivíduos, populações e espécies tendem a usar e selecionar habitats de modo não-aleatório. Consequentemente, a perda e a degradação de habitats geram impactos distintos sobre os organismos dependendo de seus atributos. Os efeitos da perda de habitat são claros – os organismos são eliminados ou desalojados por falta de habitat ou baixo sucesso reprodutivo. As consequências da degradação de habitat são mais sutis, e resultam na incapacidade de um ecossistema sustentar determinadas espécies. Como a perda e a degradação de habitat reduzem a disponibilidade de nichos, espera-se que táxons ecologicamente especializados e com requerimentos estreitos de nicho sejam mais propensos à extinção que generalistas. Organismos que são negativamente afetados por perda e degradação de habitat em geral exibem porte muito grande ou muito pequeno, baixa mobilidade, baixa fecundidade, reduzido recrutamento e estreitos requerimentos de nicho. Campos temperados constituem ambientes particularmente afetados por perda e degradação de habitat. No sudeste da América do Sul, como em muitas outras regiões do planeta, a expansão da agricultura e silvicultura são os principais responsáveis pela perda de habitat campestre. Os remanescentes de vegetação natural são usados para criação de gado, estando sujeitos à degradação pelo sobrepastejo, pisoteio e técnicas de manejo. Avaliar como a perda e degradação de habitat afetam a diversidade de organismos campestres é vital para o desenvolvimento de estratégias de conservação e manejo. A presente tese tem por objetivo investigar como a degradação e perda de habitat induzidas pela pecuária e silvicultura afetam a diversidade e a composição das comunidades de aves. Inicialmente, exploramos as relações entre variáveis de habitat e a composição da comunidade de aves num gradiente de altura da vegetação determinado por pastejo em campos litorâneos do Rio Grande do Sul. Posteriormente, avaliamos como variações no relevo interagem com variáveis de habitat e afetam a diversidade de aves em áreas de pecuária na Campanha gaúcha. Finalmente, avaliamos de que forma a perda de habitat resultante do estabelecimento de plantações industriais de celulose em áreas de campo afeta a composição de comunidades de aves campestres. Nossos resultados demonstram que a degradação de habitat decorrente do manejo de gado em campo nativo afeta a comunidade de aves de forma diferencial. Aves adaptadas a

campos ralos ou generalistas tendem a ser beneficiadas pelo pastejo, ao passo que as espécies associadas à vegetação alta e densa são desfavorecidas. As variações na topografia reduzem os impactos da degradação de habitat nos campos. Essas variações interagem com o habitat e afetam de forma diferencial os distintos componentes da diversidade. Por outro lado, a perda de habitat decorrente da silvicultura gera um impacto de maior magnitude, alterando a composição das comunidades de aves e favorecendo aves não-campestres. Nesse contexto, impedir que novas áreas de campo nativo sejam convertidas em plantações de árvores passa a ser imperativo. Embora o manejo do gado aumente a diversidade em nível de paisagem ao criar um mosaico de manchas de vegetação de alturas distintas, maior atenção deve ser dada à manutenção e recuperação de formações densas de herbáceas de grande porte. Isso somente pode ser assegurado através de mudanças no regime do pastejo ou do desenvolvimento de técnicas de manejo alternativas.

Palavras-chave: nicho ecológico, ecologia de comunidades, perda e degradação de habitat, pecuária, manejo, capim-alto, capim-baixo, especialistas de habitat, ordenação canônica, seleção de modelos, celulose, impacto ambiental, Impacto-Referência, eucalipto, campo.

ABSTRACT

Individuals, populations and species tend to select habitats in a non-random way. Consequently, habitat loss and degradation will have different impacts on organisms according to their traits. The effects of habitat loss are straightforward – organisms are eliminated or displaced because of the inexistence of adequate habitat or of low breeding success. Effects of habitat degradation are more subtle and result in the reduction of the capacity of an ecosystem to support some subsets of species. Since habitat loss and degradation reduce niche availability, ecologically specialized taxa with narrow niche requirements are expected to be more extinction prone than habitat generalists. Temperate grasslands have been strongly impacted by habitat loss and degradation. In southeastern South America, the expansion of agriculture and industrial pulpwood plantations are the main sources of habitat loss. Remnants of natural grassland vegetation are used for livestock ranching, being subject to habitat degradation from overgrazing, trampling and inadequate management techniques. The evaluation of how habitat loss and degradation affect the diversity of grassland organisms is vital for the development of management and conservation techniques. The main goal of this thesis is to evaluate how habitat degradation and loss related to cattle ranching and pulpwood plantations affect the diversity and composition of bird communities. We began by exploring the relationship between habitat variables and the composition of the bird community along a gradient of vegetation height determined by grazing in coastal grasslands of the state of Rio Grande do Sul. We then assessed how variations in the relief interact with habitat variables e affect the diversity of birds in rangelands of the *Campanha gaúcha*. Finally, we evaluated how habitat loss related with grassland afforestation for pulpwood plantations affects the composition of grassland bird communities. Our results demonstrate that habitat degradation resulting from livestock ranching in natural grasslands affects bird communities in a differential way. Birds adapted to stunted grasslands or habitat generalists tend to benefit from grazing, whereas tall-grass specialists are negatively affected. Variations in topography are responsible for reducing the impacts of habitat degradation in grasslands. These variations interact with habitat and have a differential effect on distinct components of diversity. On the other hand, the magnitude of the

impact of habitat loss from afforestation is larger, altering the composition of bird communities and favoring a series of non-grassland species. In this sense, protecting remaining grasslands from afforestation is imperative. Although cattle ranching increases diversity at the landscape level by creating a mosaic of vegetation patches of different height, more attention should be given in maintaining and recovering dense formations of tall grassland plants. This can only be achieved by changing grazing regimes or developing alternative management techniques.

INTRODUÇÃO

Habitat – Conceituação e Aspectos Teóricos

"Habitat" é um dos termos mais utilizados em ecologia, e também um de maior ambiguidade (Morris, 2003). O termo habitat tem íntima relação com o desenvolvimento da teoria de nicho, confundindo-se semanticamente a partir das definições de Grinnell (1917). Para o referido autor, o nicho de uma espécie é definido pelo habitat onde ela ocorre, sendo a soma dos requerimentos de habitat que possibilitam que a mesma sobreviva e reproduza (Grinnell, 1917). Numa tentativa de melhor delimitar esses conceitos, abordagens recentes condicionam o conceito de nicho Grinnelliano ao emprego de variáveis de nicho que são fundamentalmente não-interativas (i.e., não incluem variáveis relacionadas a interações entre os organismos), enquanto o uso de variáveis de nicho interativas caracterizariam o nicho Eltoniano (Soberón, 2007).

Hoje em dia reconhece-se que o conceito de habitat deve explicitamente considerar os recursos que contribuem para aumentar a aptidão do organismo, em vez de simplesmente descrever o local ou as condições prevalentes onde ele ocorre (Mitchell e Hebblewhite, 2012). Assim, por habitat entende-se uma área espacialmente delimitada, dentre um subconjunto de condições físicas e abióticas, onde a densidade de indivíduos que interagem, e ao menos um dos parâmetros de crescimento populacional, difere em relação a subconjuntos adjacentes (Morris, 2003). Nesse sentido, o habitat é definido pelas espécies e populações de interesse, e de uma maneira que reflete os processos subjacentes operando em escalas espaciais e temporais adequadas (Morris, 2003). Dentre esses processos destacam-se a dinâmica populacional e os mecanismos intra e interespecíficos que influenciam a abundância e a distribuição local dos indivíduos (Morris, 2003).

Habitat – Uso e Seleção

Por uso de habitat compreende-se o modo como um organismo usa os recursos e condições em um habitat (Krausman 1999). Nesse contexto, o uso de habitat é a distribuição observada dos organismos nos habitats, e, consequentemente, pode ser medida. O habitat pode ser usado para forrageamento, reprodução, escape de

predadores, descanso e outros aspectos importantes do ciclo-de-vida (Krausman 1999). A distintas categorias relacionadas ao uso de habitat muitas vezes sobrepõem-se ou alternam-se de acordo com escalas espaciais e temporais (Krausman 1999). Por outro lado, a seleção de habitats refere-se ao processo no qual os indivíduos preferencialmente usam, ou ocupam, um conjunto não-aleatório de habitats disponíveis na paisagem (Morris 2003).

O conhecimento sobre o uso e a seleção de habitat pelos organismos é vital para a compreensão de padrões e processos que ocorrem em múltiplos níveis ecológicos. Isso inclui a abundância e distribuição dos indivíduos, a dinâmica de suas populações, e a montagem e estruturação das comunidades. Visto que os indivíduos tendem a usar ou ocupar um conjunto não-aleatório de habitats disponíveis, isso gera importantes consequências para a regulação das populações e a persistência das populações no tempo (Morris 2003). Em nível de comunidades, as diferenças no uso e seleção de habitat por uma série de espécies que interagem acabam mediando a coexistência e afetando a diversidade (Morris 2003, Tews et al. 2004).

Habitat, Comunidades e Diversidade

Embora tenha sua origem no âmbito da ecologia de organismos, a teoria de habitat e a correlata teoria de nicho tem sido largamente utilizadas em ecologia de comunidades. Associações entre organismos que co-ocorrem em dada localidade e variáveis de habitat constituem a base dos estudos pioneiros de Gleason (1926) e Whittaker (1965, 1967) sobre ecologia de comunidades de plantas. Associações entre animais e habitats em nível de comunidades foram amplamente exploradas por Robert MacArthur (e.g., MacArthur e MacArthur, 1961; MacArthur *et al.*, 1966; MacArthur e Wilson, 1967). Uma das mais importantes formulações teóricas sobre a influência do habitat sobre propriedades emergentes das comunidades refere-se à hipótese da heterogeneidade de habitats, que postula uma relação positiva entre o número de habitats e a diversidade de organismos (MacArthur e MacArthur, 1961).

A diversidade de organismos tende a aumentar com a heterogeneidade de habitats em resposta ao aumento no número de dimensões de nichos particionáveis (Tews *et al.*, 2004; Cramer & Willig, 2005). Entretanto, como há um compromisso entre a heterogeneidade de habitats e a quantidade de habitats disponíveis para as espécies

individuais, essa relação é unimodal em vez de monotônica (Allouche *et al.*, 2012). Assim, em níveis muito elevados de heterogeneidade de habitats, a diversidade cai devido a um aumento nas extinções estocásticas decorrentes do pequeno tamanho populacional das espécies (Allouche *et al.*, 2012).

Dois mecanismos são responsáveis pelo aumento da diversidade em habitats heterogêneos (Cramer e Willig, 2005). Primeiro, uma variedade de habitats grandes o suficiente para sustentar populações de muitas espécies possibilita a co-ocorrência de generalistas e especialistas com diferentes preferências de habitat (Rosenzweig, 1981; Cramer e Willig, 2005). Isso não somente aumenta a diversidade pelo incremento no número de especialistas, mas também pela redução da competição entre os generalistas (Cramer e Willig, 2005). Segundo, a presença de pequenas manchas de tipos distintos de habitat pode aumentar a qualidade geral do tipo prevalente de habitat (a matriz) para determinadas espécies ao disponibilizar espaço livre de predadores ou recursos complementares (Cramer e Willig, 2005). Assim, a diversidade aumenta porque essas manchas pequenas incrementam a qualidade da matriz para algumas espécies, permitindo que persistam na comunidade (Cramer e Willig, 2005).

Os efeitos da heterogeneidade de habitat sobre a diversidade variam de acordo com o tipo de comunidade envolvida. Em comunidades vegetais, embora relações positivas tenham sido reportadas, há um acúmulo de evidências demonstrando que relações negativas são comuns (Lundholm, 2009; Douda *et al.*, 2012). Em comunidades animais, a grande maioria dos estudos revelou uma associação positiva entre a heterogeneidade de habitat e a diversidade (Tews *et al.*, 2004).

As feições de habitat que aumentam a diversidade também variam de acordo com o tipo de comunidade avaliada. Feições de heterogeneidade espacial que aumentam a diversidade de plantas estão relacionadas principalmente à propriedades físicas e químicas do solo (Lundholm, 2009; Douda *et al.*, 2012). Em comunidades animais, a heterogeneidade da vegetação e a presença de "estruturas-chave" – estruturas espaciais distintas daquelas prevalentes numa localidade e que proveem recursos, abrigo ou bens e serviços cruciais para espécies outras que aquelas típicas da localidade – são os principais responsáveis pelo aumento na diversidade (Tews *et al.*, 2004).

Impactos Antrópicos sobre o Habitat e Consequências para a Biodiversidade

Visto que feições de habitat são importantes para a diversidade de organismos, sua remoção ou simplificação gera consequências negativas para as comunidades bióticas. De fato, a perda e degradação de habitats são os principais fatores responsáveis pela atual erosão de biodiversidade (Groom e Vynne, 2006). Por perda de habitat entende-se a conversão ou transformação do habitat natural em habitats antropogênicos, ao passo que degradação de habitat refere-se ao decréscimo na qualidade do habitat gerado por atividades humanas (Groom e Vynne, 2006). Esses fatores afetam a biodiversidade através da eliminação, deslocamento ou modificação de populações de espécies nativas ou invasoras, alterando a estrutura de comunidades e ecossistemas (Groom e Vynne, 2006). Como a perda e a degradação de habitat reduzem a disponibilidade de nichos, espera-se que táxons ecologicamente especializados e com requerimentos estreitos de nicho sejam mais propensos à extinção que generalistas (Owens e Bennett, 2000; Butler *et al.*, 2007). Atributos compartilhados por organismos que são afetados negativamente por perda e degradação de habitat incluem o porte muito grande ou muito pequeno, baixa mobilidade, baixa fecundidade, reduzido recrutamento e estreitos requerimentos de nicho (Beissinger, 2000; Groom e Vynne, 2006; Noss *et al.*, 2006). Espécies que prosperam em ambientes destruídos ou alterados geralmente são generalistas de habitat, incluindo organismos invasores de ampla distribuição (Beissinger, 2000; Groom e Vynne, 2006; Noss *et al.*, 2006).

Embora os efeitos da eliminação de habitat para os organismos sejam fáceis de compreender, a degradação é mais sutil, principalmente porque a essência do conceito envolve definir e medir a qualidade do habitat. Uma das consequências da aplicação desse conceito é que ele acaba por ser espécie-específico (Groom e Vynne, 2006). Assim, a degradação de habitat pode ser benéfica para algumas espécies, mas negativa para outras, dependendo do tipo e da magnitude do impacto e dos atributos dos organismos afetados (Groom e Vynne, 2006). Além dos efeitos diretos relacionados à incapacidade de certas espécies subsistirem em ambientes modificados, a degradação de habitat também gera efeitos indiretos (Marzinelli *et al.*, 2011). Ambientes degradados muitas vezes favorecem a invasão de espécies alóctones, que podem eliminar via competição, predação ou transmissão de patógenos as espécies nativas capazes de persistir nas condições alteradas (Marzinelli *et al.*, 2011). Embora os

impactos associados à degradação de habitat sejam em geral temporários e reversíveis, eles podem ser agravados por sinergia e inércia (Groom e Vynne, 2006). Assim, interações com outros efeitos que não a causa principal de degradação e o retardo temporal existente entre a eliminação da fonte de impacto e a completa recuperação do habitat podem ampliar os efeitos negativos sobre a diversidade (Groom e Vynne, 2006). Um agravamento na magnitude desses impactos pode converter a degradação de habitat em permanente destruição (Groom e Vynne, 2006).

Perda e a Degradação de Habitat em Ambientes Campestres

A perda e a degradação de habitat têm sido particularmente severos em campos temperados (Henwood, 2010). Esse bioma, caracterizado pela predominância de vegetação herbácea, recobre aproximadamente 8% da superfície terrestre e constitui um dos ambientes mais propícios ao assentamento humano (Henwood, 2010).Existem várias denominações locais para esse bioma: pradarias no centro da América do Norte, estepes na Europa oriental e Ásia central, *Veld* na África do Sul, *Downs* na Austrália, e puna, pampas e campos na América do Sul. Cerca da metade da extensão global do bioma foi convertido em áreas agrícolas, silvicultura e paisagens urbanas (Henwood, 2010). Considerando que apenas 4,6% da superfície dos campos temperados encontra-se protegido por reservas, esse bioma ostenta o título de mais ameaçado e destruído em nível global (Hoekstra *et al.*, 2005).

Na América do Sul, os campos temperados recobrem partes do planalto Andino, Patagônia e a região do Rio da Prata, entre as porções meridionais do Paraguai e Brasil, ao Uruguai e província de Buenos Aires e regiões limítrofes, na Argentina (Henwood, 2010). Os campos temperados do sudeste da América do Sul, na região do Rio da Prata, constituem os mais ameaçados da América do Sul, tendo perdido aproximadamente 60% de sua cobertura original (Henwood, 2010; Azpiroz *et al.*, 2012). Os principais remanescentes de campo situam-se na porção norte dessa região, especialmente no setor "campos" do nordeste da Argentina, Uruguai e sul do Brasil (Vega *et al.*, 2009). Somente 0,2% dos "campos" são protegidos (Henwood, 2010), uma situação alarmante considerando que esses campos são altamente biodiversos e abrigam diversos táxons ameaçados e endêmicos (Overbeck *et al.*, 2007).

Praticamente todos os remanescentes naturais de vegetação na região dos "campos" são utilizados como pastagem para o gado. Embora essa atividade seja considerada compatível com a conservação quando comparada à agricultura e silvicultura (Develey *et al*., 2008), o pastejo contínuo do gado em porções cercadas de campo acaba por alterar a estrutura e a composição da vegetação (Altesor *et al*., 2006; Herrera *et al*., 2009), o que pode resultar em degradação de habitat e perda de diversidade. Ademais, por problemas econômicos no mercado da carne, os remanescentes campestres na região dos "campos" estão sendo convertidos em plantações industriais de eucalipto para celulose (Overbeck *et al*., 2007; Gautreau e Vélez, 2011), aumentando ainda mais a perda de habitat e comprometendo a conservação da biodiversidade.

Aves Campestres no Sudeste da América do Sul

Os campos do sudeste da América do Sul abrigam uma rica avifauna, havendo registros de 109 espécies, das quais 82 usam formações campestres de forma regular (Azpiroz *et al*., 2012). Dessas, 22 são consideradas ameaçadas ou quase-ameaçadas de extinção em nível global (Birdlife International, 2013), e diversas outras sofreram retrações populacionais locais (Azpiroz *et al*., 2012). Além de perda e degradação de habitat, o uso inadequado de agroquímicos, a poluição e a captura e caça ilegal constituem as principais ameaças (Azpiroz *et al*., 2012).

Uma revisão da literatura sobre aves campestres dessa região revelou um grande viés geográfico, com predominância de estudos realizados na Argentina (Azpiroz *et al*., 2012). Também há viés em termos de temática, com muitos estudos focando em distribuição geográfica, ameaças e requerimentos de algumas espécies (Azpiroz *et al*., 2012). Dentre os temas com carência de conhecimento figura a avaliação do uso de habitat, além de aspectos referentes à sobrevivência e genética (Azpiroz *et al*., 2012). A falta de informação sobre uso de habitat compromete não só aspectos ligados ao manejo e conservação de aves em remanescentes públicos e privados, mas também afeta avaliações relacionadas à resposta da avifauna a esforços de restauração de ambientes campestres (Azpiroz *et al*., 2012).

Objetivos e Estrutura da Tese

A presente tese versa sobre as relações entre a diversidade de aves e variáveis de habitat em campos temperados do sudeste da América do Sul. O objetivo geral é investigar como distintas variáveis de habitat afetam a estrutura das comunidades de aves campestres nessa região. Em termos específicos, a tese avalia como a degradação e a perda de habitat campestre induzida pela pecuária e a silvicultura afetam a diversidade e a composição das comunidades de aves. As principais inovações teóricas referem-se à elucidação de como diferentes componentes da diversidade são afetados pela perda e degradação de habitat. Em termos práticos, os resultados contribuem para o desenvolvimento de estratégias de manejo e conservação da biodiversidade em campos temperados utilizados para pecuária e silvicultura. Tais contribuições são desenvolvidas ao longo de três capítulos. No primeiro, intitulado "*Habitat features determining the composition of avian communities along a structural gradient of grassland vegetation in coastal rangelands of southern Brazil*", são testadas relações entre variáveis de habitat e a composição de espécies de aves ao longo de um gradiente de pastejo em campos litorâneos no sul do Rio Grande do Sul, visando determinar que atributos de habitat são mais importantes na estruturação da comunidade e como distintos grupos de aves respondem a diferenças nas variáveis de habitat. O segundo capítulo tem por título "*Topography and habitat features determine different components of bird diversity in grasslands of southern Brazil*" e investiga, numa abordagem de teoria da informação, como a interação entre o habitat e a topografia determinam o número e a composição de espécies de aves em áreas de pecuária com distintas estruturas de vegetação campestre na região da Campanha Gaúcha. Por fim, no capítulo intitulado "*Shifts in composition of avian communities related to temperate-grassland afforestation in southeastern South America*", é avaliada como a perda de habitat campestre resultante do plantio de árvores para produção de celulose afeta a composição da comunidade de aves do sul do Rio Grande do Sul. A última seção, "*Considerações finais*", integra os resultados dos capítulos individuais. Cada capítulo está formatado de acordo com as normas dos periódicos para onde foram ou serão encaminhados. Portanto, cada um possui uma formatação distinta.

CAPÍTULO 1

HABITAT FEATURES DETERMINING THE COMPOSITION OF AVIAN COMMUNITIES ALONG A STRUCTURAL GRADIENT OF GRASSLAND VEGETATION IN COASTAL RANGELANDS OF SOUTHERN BRAZIL

Co-autores: Andros T. Gianuca, Vinicius A. G. Bastazini e Sandra C. Müller.

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ABSTRACT

Individuals, populations and species tend to use or select habitats in a non-random way. Consequently, habitat loss and degradation resulting from anthropogenic impacts will have differential effects on organisms according to their degree of habitat specialization. Temperate grasslands have experienced high levels of habitat loss, especially in southeastern South America. Remnants of grassland vegetation are used for livestock ranching and subject to habitat degradation resulting from trampling and grazing. Assessing how habitat features affect the composition of grassland faunal communities is a first step to understand the role impacts resulting from current cattle-ranching management practices upon biodiversity. In this paper, we used canonical ordination techniques to test for relationships between habitat variables and the composition of bird communities in coastal temperate grasslands of southern Brazil. We used a 500 x 120 m plot to sample birds. Our sample consisted of eight plots located in short-grass pastures, twelve in tall-grass pastures and thirteen in pastures of intermediate height. We measured five variables describing habitat. We recorded 1,528 individuals and 25 species of birds in plots. The first ordination axis indicated a strong contribution of mean vegetation height on the composition of the bird community, while the second axis revealed the influence of herbaceous vegetation patchiness and woody vegetation cover. Three groups of species were revealed by the ordination: one comprised by tall-grass specialists, another associated with short grass, and a third associated with vegetation patchiness and woody vegetation. Tall-grass specialists are the species most impacted from habitat degradation resulting from trampling, mowing and burning of tall and unpalatable tussocks. Persistence of these species is related with presence of swales immediately behind the dune system and where remnants of tall vegetation occur. Short-grass specialists, on the other hand, benefit from overgrazing, trampling and removal of tall vegetation. Woody vegetation is an important keystone structure, which enables the occurrence of a series of passerines in grasslands. Although livestock ranching promotes regional diversity by creating distinct patches of vegetation height in grasslands, current management practices directed to the maintenance of short-grass pastures may eliminate an entire subset of species and reduce diversity. We recommend that management should focus

on maintaining large patches of tall-grass habitat within pastures through rotational grazing or exclusion of cattle from tall-grass remnants.

Key words: livestock ranching, management, tall-grass, short-grass, habitat specialists, canonical ordination, "*campos*" grasslands

INTRODUCTION

Knowledge on habitat use and selection by organisms is vital for understanding the abundance and distribution of individuals, the dynamics of their populations, and how communities are assembled and organized. More than just a reference to a spatially bounded area, the concept of habitat is intimately linked to the species and populations of interest, as well as the underlying processes of population dynamics and intra- and interspecific mechanisms that influence the local abundance and distribution of individuals (Morris 2003). Since individuals tend to use or occupy a non-random set of available habitats in a landscape, this has important consequences for population regulation and the persistence of populations in time (Morris 2003). At the community level, differential habitat use and selection among a series of interacting species is a key factor in determining coexistence and diversity (Morris 2003, Tews et al. 2004).

Populations of the same species may live in different environments and vary in their habitat preferences (Morris 2003), the same holding true for different species in a set of communities. Species may exhibit a wide array of habitat tolerances (habitat generalists), while others have very specific and narrow habitat preferences (habitat specialists) (Gaston 1994). Taken together, these assets mean that habitat loss and degradation associated with anthropogenic impacts will have differential effects depending on how different organisms use and select habitat. Since habitat loss and degradation usually reduce niche availability, ecologically specialized taxa are more extinction prone than habitat generalists (Owens and Bennett 2000).

Temperate grasslands worldwide have experienced major habitat loss and degradation resulting from the expansion of agriculture, pulpwood plantations and inadequate cattle ranching management practices (Henwood 2010). This situation has

been particularly severe in southeastern South America, where temperate grasslands span 762,000 km^2 from southern Paraguay and Brazil through Uruguay and eastern Argentina (Azpiroz et al. 2012). The largest remnants are located in the "*campos*" unit of northeastern Argentina, Uruguay and southern Brazil (Vega et al. 2009). These grasslands are highly biodiverse and harbor many endemic taxa (Overbeck et al. 2007).

Birds are one of the most threatened groups of temperate grassland organisms (Goriup 1988, Askins et al. 2007, Azpiroz et al. 2012). The main reasons for these declines are related to habitat loss and degradation (Vickery and Herkert 2001, Fisher and Davis 2010, Azpiroz et al. 2012). Since threats affect the availability and quality of habitats, investigations addressing grassland-bird habitat relationships have been a recurrent topic (Fisher and Davis 2010). One of the main conclusions of studies investigating avian communities is that groups of species tend to respond differently to variations in biotic and abiotic features of grasslands (Derner et al. 2009, Fisher and Davis 2010, Azpiroz et al. 2012). The heterogeneity of the vegetation and the presence of "keystone structures" – distinct spatial structures that provide resources, shelter, or goods and services crucial for other species – are the main habitat features that influence the diversity and composition of avifaunal communities in grasslands (Tews et al. 2004, Fisher and Davis 2010). These variables, in turn, are mediated by complex interactions between 'ecosystem engineers' such as grazers and burrowers, and fire and drought regimes (Ceballos et al. 1999, Fuhlendorf et al. 2009, Allred et al. 2011).

Most studies on grassland-bird habitat relationships were carried out in North America and Europe, and have spawned important management and conservation techniques (Fisher and Davis 2010, Báldi and Batáry 2011). Nearly all studies addressing this issue in South America were set in the argentine pampas (Azpiroz et al. 2012). Lack of thorough knowledge on relationships between habitat features and faunal communities throughout temperate grasslands of southeastern South America is troublesome for two basic reasons. First, only 40–45% of the original grasslands remain, and what is left is being rapidly converted into soybean and tree plantations (Henwood 2010, Azpiroz et al. 2012). Second, since virtually all of the remaining grasslands are used for livestock ranching, remnants of natural vegetation are subject to habitat degradation resulting from grazing and trampling. Considering that only 1% of the grasslands is protected, conservation of grassland biodiversity depends largely

on the development of sound livestock management techniques to be implemented in privately owned rangelands (Develey et al. 2008, Azpiroz et al. 2012).

In the present contribution, we assessed how habitat features drive the composition of avian communities in temperate coastal grasslands of southern Brazil. Our study system is characterized by differences in vegetation structure, which result mainly from variations in grazing intensity and the micro-relief. We used canonical ordination techniques to test how vegetation attributes and structural features of grasslands influence the abundance and composition of bird communities, seeking relationships between species and important characteristics of the vegetation as well as eventual keystone structures. Our main goal was to determine which groups of species were specialized in habitat features that could be negatively affected by habitat degradation associated with cattle-ranching management practices.

METHODS

Study area. We sampled an extension of 1,556 ha of coastal grasslands in extreme southern Brazil around Cassino seaside resort (32°11'S, 52°10'W), Rio Grande municipality, Rio Grande do Sul state. Grasslands lay immediately behind coastal dunes and cover sandy soils exhibiting a complex system of shallow depressions. Deeper swales covered with wetland vegetation cross the area. Before the consolidation of the livestock industry in the region, in the XIX Century (Vieira and Rangel 1988), grasslands were probably dominated by herbs and forbs 50–100 cm tall, as inferred from observations in cattle-free areas in and around the urban sector of Cassino. Stunted herbaceous vegetation appeared to have been naturally limited to some sectors of better-drained terrain, especially on the crests of ancient transgressive dune fields. Currently, livestock grazing and, to a lesser extent, fire are the main drivers of vegetation structure in our study area. Adjustment of the number of cattle in pastures (*i.e.*, a large fenced portion of the grassland where livestock is confined) is the main livestock management practice. Use of fire is occasional and limited to some ranches, especially where tall and dense unpalatable vegetation occurs. These management practices usually result in pastures that have two strata: one of short vegetation 1–20 cm tall, and a taller layer of unpalatable tussocks and forbs, which can reach up to 70

cm. Homogeneous short-grass patches are found in a few overgrazed pastures. In some sectors large remnant patches of homogeneous tall-grasses occur. The presence of these patches is largely influenced by the micro-relief, since they tend to be located mainly in small depressions, which predominate immediately behind the coastal dune system.

Grasslands are dominated by Poaceae, with Cyperaceae covering wetter sectors in depressions (Boldrini 2009). *Androtrichum trigynum* (Spreng.) H.Pfeiff (Cyperaceae) and *Juncus acutus* L. (Juncaceae) are the dominant species of the tall stratum. Scattered shrubs, cactus and small trees occur throughout our study area, as well as small eucalyptus stands. Cattle and to a lesser extent horses are ranched in grasslands. Exotic grasses are not planted in pastures.

Climate in the region is humid to sub-humid; mean annual precipitation is approximately 1200 mm, and mean annual temperature is 18°C (IBGE 1986). Precipitation is slightly higher in the winter and spring, and water deficit can occur during dry summers (IBGE 1986). Depressions in grasslands are flooded by rains in autumn-winter and most dry out in the summer.

Sampling design. Pastures were selected for sampling based on size and vegetation structure. We used a 500 x 120 m plot to sample birds. We followed a systematic sampling scheme, locating the first plot at the entrance of the pasture and placing the others sequentially at 200 m intervals to avoid double-counting individuals. A minimum distance of 200 m was maintained in relation to fences, wetlands and patches of trees to avoid edge effects (Reese and Ratti 1988). Isolated saplings and cactuses were included in plots. Our initial goal was to ensure that plots were allocated equally in pastures according to vegetation height. Due to logistic constraints imposed by the size of pastures and management practices, our final sample consisted of eight plots located in short-grass pastures (mean vegetation height <10 cm), twelve in tall-grass pastures (> 20 cm) and thirteen in pastures of intermediate height.

Bird counts. Sampling was carried out between 31 October and 05 November 2008. We restricted counts to the peak of the breeding season of the local avifauna (Belton 1994) in order to maximize detection and minimize the probability of double-counting individuals, since birds are expected to be more vocal and restricted to territories during this time of the year (Bibby et al. 1992). We used the area-search

method (Ralph et al. 1993) to count birds. In this method one or more observers walk for 20 min through three search areas inside a plot of variable size, searching for quiet birds and unfamiliar vocalizations (Ralph et al. 1993). We modified the size and shape of the plot as well as the number of search areas, and did not use a time-based stopping rule as proposed by Watson (2003). The area-search method has been used to count birds in grassland habitats, and the enhancement of the detectability of secretive species is one of its main advantages (Dieni and Jones 2002, Atkinson et al. 2006, Roberts and Schnell 2006).

Two observers (RAD and AG) counted birds simultaneously within a plot. Once the location of the plot had been defined, each observer was responsible for sampling a 500 x 60 m half-section of the plot. We progressed along the full length of the plot, passing through each sector only once. We walked at the same pace and communicated frequently to ensure that individual birds were not double-counted. Following Roberts and Schnell (2006), we walked within 10 m of all points inside the perimeter of the plot. It took us approximately 15 minutes to sample each plot.

All individuals seen or heard were counted. Birds foraging or displaying in flight up to 30 m were included, with the exception of martins and swallows, whose small size and agile flight hampered our ability to avoid double-counting them between and within plots. Counts were carried out in the first four hours after sunrise in clear days with wind speed lower than 5 on the Beaufort scale to avoid bias (Bibby et al. 1992, McCoy et al. 2001). We used 12 x 50 binoculars to help locate birds and a hand-held GPS unit with a 5 m error to determine distances.

Habitat variables. Our approach was to use a reduced number of habitat features selected on the basis of their importance to grassland birds (Fisher and Davis 2010), ensuring that the variability of habitats used by multiple species was contemplated (Wiens 1969). Definitions of variables follow Fisher and Davis (2010). We measured the height of the herbaceous vegetation with a ruler at 5-m intervals along nine linear transects spaced 50 m apart and orientated perpendicularly in relation to the main length of the plot. A total of 216 measures were obtained per plot. We calculated the mean and used the CV as a measure of patchiness. We visually determined the proportion of bare ground in each 25 x 25 m section of the plot and pooled values to obtain a total estimate. This same procedure was used to determine the cover of

standing water and of woody vegetation. Woody vegetation included all isolated saplings, shrubs and clumps of cactuses taller than the canopy of the surrounding herbaceous vegetation.

Data analyses. We built a correlation matrix to check for multicollinearity (Legendre and Legendre 1998) in our set of habitat variables. All pairs of variables presented correlation coefficients <50% and were kept in our models.

We used Canonical Correspondence Analysis (CCA) (ter Braak 1986) to explore the relationship between habitat variables and the composition of the bird community. CCA is a method of direct gradient analysis, which maximizes the linear relationship between a set of multiple independent variables and another of dependent variables (ter Braak 1986, Legendre and Legendre 1998). We evaluated the significance of the first canonical axis and of all canonical axes together using a Monte Carlo method, permutating the model residuals (9,999 permutations) under the reduced model (see Lepš and Šmilauer 2003). The null hypothesis assumes no relation between species and habitat variables. Bird counts were square root transformed. We only analyzed species recorded in three or more plots (incidence ≥ 9%). Values of rare species were down-weighted to minimize their influence on the analysis (Lepš and Šmilauer 2003). Axes scaling focused on inter-species distance. The CCA ordination was carried out in CANOCO 4.5 statistical software (ter Braak and Šmilauer 2002).

RESULTS

Habitat variables. Mean vegetation height was highly variable among plots, ranging from 5.63-57.0 cm. Vegetation height tended to be less patchy in sectors with prevalence of tall grass (Fig. 1). We recorded patches of bare ground in 18 plots. The total area of exposed ground per plot ranged from 5–8,100 m^2. Woody plants were observed only in eight plots and covered 5–180 m^2 per plot, whereas water-filled depressions were found in six plots and ranged from 10–200 m^2. The cover of woody plants was larger in sectors where vegetation height was patchier. Water-filled depressions were located solely in short-grass pastures.

Bird community. We recorded 1,528 individuals and 25 species of birds with incidence values ≥ 9% (Appendix I). The Southern Lapwing (*Vanellus chilensis*) and the Grassland Yellow Finch (*Sicalis luteola*) were the most abundant and frequent species.

Bird-habitat relationships. The first two axes of the CCA explained 31.2% of the variation of the species data and 84.4% of the relationship between species and habitat variables (Fig. 2). The global test of significance showed that the canonical relationship between both matrices was highly significant (first canonical axis: *F-ratio* = 8.88; *p* = 0.0001; all canonical axes: *F-ratio* = 3.17; *p* = 0.0001). There was a strong correlation between habitat variables and species composition in the first two axis (*r* = 0.962 and *r* = 0.867, respectively). The first axis indicated a strong contribution of mean vegetation height on the composition of the bird community, while the second axis was related with patchiness and woody vegetation cover. Bare ground and water cover had minor contributions to the variation in the composition of the bird community.

Three groups of species were revealed by the ordination. The first, more diffuse, is formed by species associated with a gradient of increasing vegetation height. Species in this group include the Sedge Wren (*Cistothorus platensis*), White-browed Blackbird (*Sturnella superciliaris*) and Lesser Grass Finch (*Emberizoides ypiranganus*), all of which were restricted to areas were vegetation was homogeneous and over 40 cm tall. The Great Pampa Finch (*Embernagra platensis*) and Grassland Sparrow (*Ammodramus humeralis*) were more abundant in sectors of slightly shorter and less dense tall grass. Species such as the Spotted Nothura (*Nothura maculosa*), Hellmayr's Pipit (*Anthus hellmayri*) and Grassland Yellow Finch occurred along a broad spectrum of vegetation height, but tended to be slightly more numerous in areas of intermediate height.

The second group was formed by species associated with grass shorter than 20 cm, such as the Southern Lapwing (*Vanellus chilensis*), American Golden Plover (*Pluvialis dominica*), Burrowing Owl (*Athene cunicularia*), Common Miner (*Geositta cunicularia*) and Short-billed Pipit (*Anthus furcatus*). Birds that forage in water or wet pastures were also part of this group, namely the White-faced Ibis (*Plegadis chihi*), Western Cattle Egret (*Bubulcus ibis*), Yellowish Pipit (*Anthus lutescens*) and Correndera Pipit (*Anthus correndera*). The Black-and-white Monjita (*Xolmis dominicanus*) was associated with homogeneous short-grass pastures.

The last group was formed by species positively associated with heterogeneous grasslands and woody vegetation. All species in this group were passerines that rely on trees and bushes for perching and nesting and forage on the ground in patches of short grass or in the air.

DISCUSSION

Our study revealed that the height of the herbaceous vegetation was the main habitat variable responsible for the patterns of species composition observed in coastal grasslands of southern Brazil. The combined effects of vegetation patchiness and presence of saplings and cactuses further played an important role in enabling the occurrence of some groups of species in our study area. Our results also indicate that birds that occur in grasslands form three distinct subsets: one of tall-grass specialists, another associated with short grass, including some wetland birds, and a third related with patchy and woody vegetation.

Vegetation height, bare-ground exposure and litter depth were the most consistent predictors of habitat use by grassland birds in a review covering studies carried out mainly in North America (Fisher and Davis 2010). In our study system, the height of the vegetation was responsible for separating subsets of species along the first axis. The importance of tall vegetation for grassland birds may be related to the provision of concealment and cover from predators or wind (Fisher and Davis 2010). In southeastern South America, tall grass is the sole habitat of 25 bird species, mostly passerines, which rely on this physiognomy to fulfill their entire life cycles (Isacch and Cardoni 2011, Azpiroz et al. 2012). These species evolved in tall-grass grasslands that, at least in our study region, apparently were the dominant grassland type before European settlement. Since tall grasses and reeds present in coastal grasslands are unpalatable for livestock, local management practices are aimed at eliminating these plants with the use of fire or mowing, or by having cattle trampling them down. Persistence of tall vegetation in the region is related to the occurrence of depressions near coastal dunes where eradication is more difficult. Our results demonstrate that birds in this group are negatively affected by habitat degradation resulting from local livestock management. Nearly all regionally or globally threatened grassland birds in

southeastern South America grasslands are tall-grass specialists or species that depend on tall, dense vegetation during some phase of their life cycles (Bencke et al. 2003, Azpiroz et al. 2012).

Patchiness of the height of the herbaceous vegetation was also an important biotic habitat variable in the ordination. Sectors with high patchiness occurred in crests of ancient transgressive dune fields, probably because livestock tends to concentrate in these areas to rest, and associated trampling and grazing creates small patches of variable vegetation height. These areas also favored the development of cactus and saplings, apparently because they were not flooded in the winter. Both variables contributed to explain the occurrence of passerines that depend on woody vegetation for perching, nesting and resting. Two of them, the Firewood-gatherer (*Anumbius annumbi*) and the Cattle Tyrant (*Machetornis rixosa*), also depend on patches of short grass to forage for invertebrates on the ground.

Heterogeneous vegetation and presence of keystone features, especially trees, are important drivers of avian diversity in grasslands (Tews et al. 2004). Small habitat patches may increase the overall quality of a pervasive habitat type (the matrix) in which they occur by supplying predator-free space or complementary resources, thus enabling the persistence of more species in the landscape (Cramer & Willig 2005). Due to their restricted size, patches of contrasting vegetation height recorded in coastal grasslands probably enhance diversity by providing complementary resources for birds. Keystone features such as saplings and clumps of cactus are likely to function in the same way.

Nearly half of the species were associated with short-grass, including heavily grazed pastures, and are likely benefiting from livestock ranching practices in the region. This includes typical short-grass specialists of South American grasslands, such as the Southern Lapwing and Short-billed Pipit, as well as some species which are able to use a broader spectrum of the vegetation-height gradient, such as the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) and the Shiny Cowbird (*Molothrus bonariensis*) (Azpiroz et al. 2012). Short-grass specialists likely had limited habitat availability in the region before the introduction of cattle, and probably expanded their ranges and populations following European settlement.

Conciliating rangeland management and grassland bird conservation has proven to be challenging because of the different habitat requirements of species, physical characteristics of grasslands, and the type of grazing regime determined by ranchers (Coppedge et al. 2008, Derner et al. 2009). In coastal grasslands of southern Brazil, a continuous grazing regime is practiced, and management techniques result in the elimination or reduction of tall-grass stands. Since ranches manage livestock at a within-pasture scale, a rotational system would be more effective in enabling the development of a mosaic of distinct habitat patches capable of fulfilling the habitat needs of multiple species (Derner et al. 2009). If rotation is economically unviable, protection of large patches of tall vegetation in sectors of pastures through exclusion of livestock may be an alternative strategy. Since cattle-free areas in grasslands of southern Brazil tend to be encroached with shrubs (Pillar and Veléz 2010), we recommend that additional studies should be conducted in order to develop management techniques to maintain the herbaceous nature of the vegetation.

Isacch and Cardoni (2011) recommended that different grazing regimes should be implemented in coastal pampas grasslands in order to maintain local and regional diversity of birds. This occurs because both short and tall-grass grasslands are important for tall and short-grass specialists of conservation concern. In our study area, short-grass grasslands are important only for the threatened Black-and-white Monjita, which also needs patches of tall, dense vegetation for breeding and roosting, and which could probably survive in pastures under a rotational grazing regime. However, important populations of the same short-grass birds recorded in coastal Buenos Aires by Isacch and Cardoni (2011) and that require large expanses of stunted grasslands occur in nearby grasslands along saltmarshes in coastal Rio Grande do Sul (Bencke et al. 2006). Management strategies directed to manage habitat both for tall and short-grass specialists, such as the one proposed for Buenos Aires, are likely to apply in these saltmarsh areas.

In conclusion, we demonstrated that habitat features associated with livestock ranching in southern Brazilian grasslands determine the occurrence of three subsets of species according to the height of the vegetation, the presence of patches of variable vegetation height, and cactuses and saplings. Current management practices are carried out at within-pasture level, and result in the elimination or reduction of

unpalatable tall grassland plants. This negatively affects the survival of tall-grass specialists, including species of conservation concern. Although livestock ranching promotes regional diversity by creating distinct patches of vegetation height in grassland, a shift in management practices, or the exclusion of cattle from patches of tall vegetation, is needed to maintain the full components of avian communities in the region.

ACKNOWLEDGMENTS

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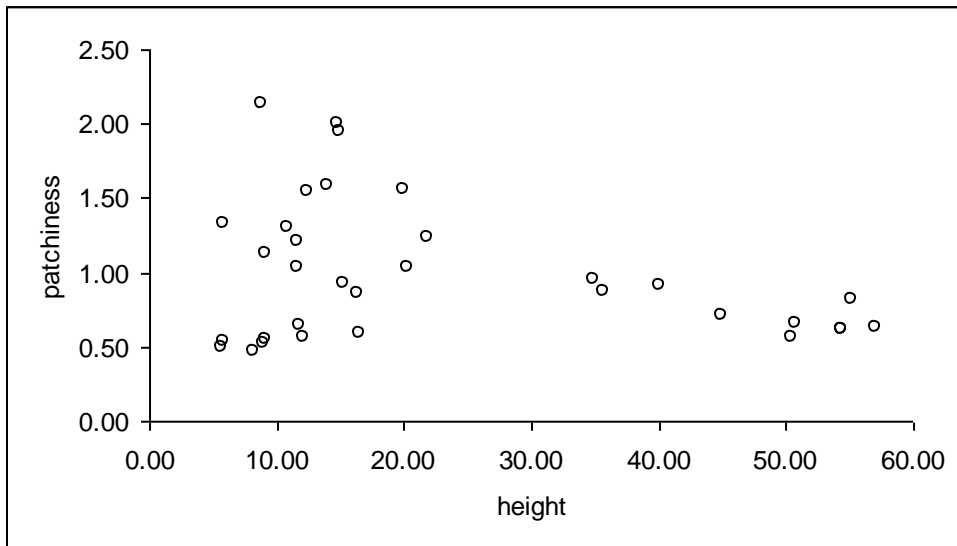
Fig. 1. Relationship between mean height (in cm) and patchiness (CV of height) of the herbaceous vegetation in 33 plots in southern Brazilian coastal grasslands. Note that taller vegetation tends to be more homogeneous.
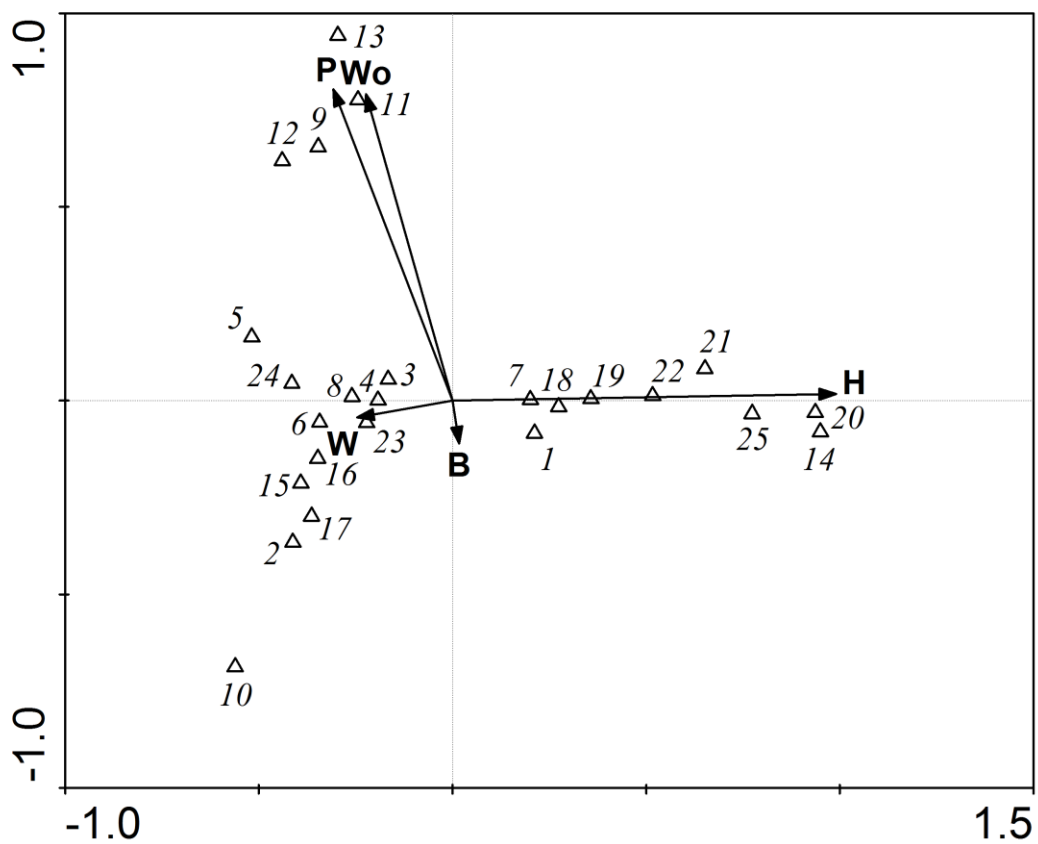
Fig. 2. Canonical Correspondence Analysis (CCA) ordination diagram showing

relationships between birds and habitat descriptors in coastal grasslands of southern Brazil. Triangles represent species and vectors represent habitat variables highly correlated with both axis. B- bare ground cover; H- mean height of herbaceous vegetation; P- patchiness of herbaceous vegetation; W- water cover; Wo- woody vegetation cover; 1- *Nothura maculosa*; 2- *Plegadis chihi*; 3- *Bubulcus ibis*; 4- *Vanellus chilensis*; 5- *Pluvialis dominica*; 6- *Athene cunicularia*;7- *Milvago chimango*; 8- *Geositta cunicularia*; 9- *Anumbius annumbi*; 10- *Xolmis dominicanus*; 11- *Machetornis rixosa*; 12- *Pitangus sulphuratus*; 13- *Tyrannus savana*; 14- *Cistothorus platensis*; 15- *Anthus lutescens*; 16- *Anthus furcatus*; 17- *Anthus correndera*; 18- *Anthus hellmayri*; 19- *Sicalis luteola*; 20- *Emberizoides ypiranganus*; 21- *Embernagra platensis*; 22- *Ammodramus humeralis*; 23- *Pseudoleistes virescens*; 24- *Molothrus bonariensis*; 25- *Sturnella superciliaris*.

Appendix I. Abundance and frequency of occurrence of bird species recorded in 33 plots in coastal grasslands of southern Brazil.

Taxon	English name	N	f (%)
Tinamidae			
Nothura maculosa	Spotted Nothura	13	31
Threskiornithidae			
Plegadis chihi	White-faced Ibis	23	9
Ardeidae			
Bubulcus íbis	Western Cattle Egret	29	16
Falconidae			
Milvago chimango	Chimango Caracara	23	31
Charadriidae			
Vanellus chilensis	Southern Lapwing	458	94
Pluvialis dominica	American Golden Plover	48	19
Strigidae			
Athene cunicularia	Burrowing Owl	24	44
Furnariidae			
Geositta cunicularia	Common Miner	5	13

Anumbius annumbi	Firewood-gatherer	21	22
Tyrannidae			
Xolmis dominicanus	Black-and-white Monjita	5	9
Machetornis rixosa	Cattle Tyrant	7	19
Pitangus sulphuratus	Great Kiskadee	6	16
Tyrannus savana	Fork-tailed Flycatcher	8	16
Troglodytidae			
Cistothorus platensis	Sedge Wren	10	16
Motacillidae			
Anthus lutescens	Yellowish Pipit	48	47
Anthus furcatus	Short-billed Pipit	111	50
Anthus correndera	Correndera Pipit	26	19
Anthus hellmayri	Hellmayr's Pipit	70	63
Icteridae			
Pseudoleistes virescens	Brown-and-yellow Marshbird	109	38
Molothrus bonariensis	Shiny Cowbird	22	22
Sturnella superciliaris	White-browed Blackbird	78	34
Emberizidae			
Ammodramus humeralis	Grassland Sparrow	4	9
Thraupidae			
Sicalis luteola	Grassland Yellow Finch	264	72
Emberizoides ypiranganus	Lesser Grass Finch	16	25
Embernagra platensis	Great Pampa Finch	46	41

CAPÍTULO 2

TOPOGRAPHY AND HABITAT FEATURES DETERMINE DIFFERENT COMPONENTS OF BIRD DIVERSITY IN GRASSLANDS OF SOUTHERN BRAZIL

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Summary

1. Our goal was to assess how topography and habitat features interact to determine avian diversity in grasslands of southern Brazil. We determined the relative contributions of topographic levels, habitat variables and their interaction upon the number of species and the composition of avian communities.

2. The undulating topography of rangelands leads to the development of mesic sectors in swales and depressions were taller grasses and forbs occur and grazing is less intense. These areas may serve as refuges for organisms specializing in tall-grass grasslands. Therefore, understanding the relative effects of habitat variables and topography on diversity will enable the assessment of the role of swales in grassland conservation.

3. We sampled birds in four sites located in the southwestern sector of Rio Grande do Sul, Brazil's southernmost state. Birds were counted in 400 x 100 m plots allocated in pastures containing mesic and dry grasslands. In each plot we estimated the cover of eight habitat variables and measured the height and vertical density of the vegetation. We used ordination techniques to explore relationships between plots and habitat variables, and relied on linear models to evaluate the effects of topography, environmental variables and their interactions upon avian species density and composition following an information-theoretic approach.

4. Swales are characterized by having greater proportion of water, bare ground (mostly mud), bush, and wetland-plant cover, and by exhibiting taller herbs that are more homogeneous in terms of vertical density. Species density depended largely on the variability of habitat features, whereas composition was entirely predicted by topography and its interaction with habitat variables.

5. Our results demonstrate that habitat features and topography have different effects on avian diversity, which leads to distinct management strategies. Since the number of bird species in grasslands depends largely on habitat complexity, intensive grazing and simplification of the vegetation structure will lead to species loss irrespective of topography. On the other hand, considering that topography and related differences in habitat variables are determining the composition of avian communities, conservation of both hilltop and swale-grasslands is necessary to maintain diversity in our study system.

Key-words: *Campos* grasslands, mesic, grazing, cattle ranching, model selection

Introduction

Habitat loss and degradation are the main drivers of biodiversity erosion (Groom & Vynne 2006). Although the effects of habitat loss upon organisms are straightforward, habitat degradation – a decrease in the quality of an area due to human interference – has more subtle consequences (Groom & Vynne 2006). Habitat degradation results in the reduction of the capacity of an ecosystem to support some subsets of species occurring in a given area (Groom & Vynne 2006). Asides from being species-specific, impacts are usually temporary and reversible, but may worsen according to the source of degradation (Groom & Vynne 2006). Although impacts of habitat degradation upon biodiversity are less severe than habitat loss, the elimination of subsets of species may lead to the collapse of ecosystem functions (Groom & Vynne 2006). Furthermore, synergistic interactions and temporal delays associated with the type and magnitude of impacts that cause alterations in the quality of habitats usually lead to further degradation that may result in permanent habitat loss (Groom & Vynne 2006; Marzinelli *et al*. 2010).

Temperate grasslands rank high among the world's most threatened ecosystems, having lost nearly half of their original cover to agriculture, afforestation and urbanization (Hoekstra *et al*. 2005; Henwood 2010). Nearly all the remaining natural grassland areas are used as rangelands, being subject to habitat degradation from trampling and overgrazing related to high pressure of cattle, horse and sheep ranching (Henwood 2010).

Rangelands in temperate grasslands are usually associated with areas of rolling topography, where agriculture is impractical. Variations in the relief usually promote the development of mesic grasslands in concave slopes and swales, and dry grasslands in adjacent hilltops (Cingolani *et al*. 2003; Sebastiá 2004). Plant communities from the extremes of this gradient differ in terms of physiognomy and species composition, with mesic grasslands being less diverse because of the high dominance of plants adapted to wetter conditions (Cingolani *et al*. 2003; Focht & Pillar 2003; Sebastiá 2004; Hallasy *et al*. 2005). Grazing plays an important role in mediating these relationships along topographic gradients in grasslands. Grazers can amplify, reduce, or preserve the relationship between vegetation and abiotic environment (Cingolani *et al*. 2003). The

relative effects of grazing and topography upon grassland plant physiognomy and diversity are determined mainly by the strength of the resource gradient and, probably, by the evolutionary history of grazing in the system (Milchunas *et al*. 1989; Cingolani *et al*. 2003).

Grassland birds are strongly affected by vegetation heterogeneity, especially differences in physiognomy at finer scales (Wiens 1969, 1974; Rotemberry & Wiens 1980). Despite the profusion of studies on habitat selection by grassland birds fueled by population declines associated to habitat loss (see Fisher & Davis 2010 and references therein), the influence of topography on the diversity of these organisms remains to be properly addressed. Empirical observations from southern Brazilian grasslands suggest that bird diversity is higher in swales than in hilltop pastures, probably due to differences in vegetation structure and type (Develey *et al*. 2008; Bencke 2009). These authors suggested that swales could function as permanent or temporary refuges for tall-grass specialists, which are absent from adjacent overgrazed hilltops. Understanding these relationships may lead to the development of management techniques capable of ensuring compatibility between cattle ranching and grassland conservation.

In this paper, we evaluated how topography, habitat features and their interactions determine the number of species and the identity of bird communities in dry pastures located on hilltops and moister grasslands in swales located in the *Campos* grasslands of southern Brazil. Since grassland birds are sensitive to habitat features, we expect that variation in habitat would be a major predictor of avian diversity.

Materials and methods

Study area

Sampling took place in four sites located in the southern portion of the *Campanha Meridional* physiographic region. Sites were centered in the following ranches: 1) Estância São Crispim (30°41'S, 53°57'W; *c*. 300 m a.s.l.), Lavras do Sul municipality, 2) Estância Primavera (30°42'S, 54°28'W; *c*. 180 m a.s.l.), 3) Estância Leões (30°59'S, 54°29'W; *c*. 250 m a.s.l.), and Estância Santa Lídia (31°09'S, 54°19'W; *c*. 300 m a.s.l.), the latter three in Dom Pedrito municipality.

Sites are characterized by gently rolling terrain covered with grasslands. Gallery forests occur along major water courses and marshy vegetation is found in floodplains and swales among the hills. Soybean and eucalyptus plantations are becoming widespread in recent years. Climate in the region is subtropical humid; the mean annual temperature is 18° C and the mean annual precipitation 1,472 mm (IBGE 1986). Despite the absence of a dry season, periods of water deficit occur frequently during dry summers (Mota *et al*. 1970).

Grasslands in the region are covered with herbaceous and shrubby vegetation, with prevalence of the families Poaceae, Asteraceae and Fabaceae (Develey *et al*. 2008). Observations on pastures (*i.e.*, large fenced portions of grasslands where livestock is confined) with very low grazing regimes suggest that tall grasses and forbs (> 50 cm) originally dominated grasslands in our study region. The distribution of naturally stunted herbaceous vegetation was probably limited to very dry hilltops, especially rocky sectors.

Current grazing regimes creates a two-layer grassland system: a lower stratum covered with prostrate plant species (most grasses, but also leguminous and forbs) with stolons or rhizomes, and a taller layer composed of caespitose grasses (tussocks), some forbs and shrubs usually patchy in terms of distribution (Overbeck *et al*. 2007). The rolling terrain determines different conditions of solar and wind exposition, soil types, and water availability, resulting in distinct plant assemblages defined by topography (Focht & Pillar 2003). The lower stratum of grasslands located on hillcrests is covered mostly by *Paspalum notatum* Flueggé (Poaceae), whereas the upper layer is represented by tussocks of *Stipa* spp., *Aristida laevis* (Nees) Kunth and *Saccharum angustifolium* (Nees) Trin. (Poaceae), the spiny forb *Eryngium horridum* Malme (Apiaceae), and shrubby species such as *Baccharis trimera* (Less.) DC (Asteraceae) and *Baccharis coridifolia* DC (Asteraceae). Mesic grasslands in swales are characterized by the presence of *Axonopus affinis* Chase (Poaceae), *Paspalum pauciciliatum* (Parodi) Herter (Poaceae), and *Eleocharis* spp. (Cyperaceae) in the lower stratum, and tussocks of *A. laevis*, *S. angustifolium*, and *Andropogon lateralis* Nees (Poaceae), and the spiny forb *Eryngium pandanifolium* Cham. & Schltdl (Apiaceae) in the upper layer. Grazing intensity and management practices, especially mowing of pastures, use of chemical

fertilizers and cattle exclusion, also affect the physiognomy and floristic composition of local grasslands.

Ranches in the region are devoted to cattle, sheep and horse ranching on natural grasslands. Animal load is adjusted according to the availability of forage throughout the year. Italian Ryegrass *Lolium multiflorum* Lam. (Poaceae) and a few other exotic grasses are sometimes sown among native pastures as a source of additional forage during the winter. Small pastures consisting entirely of exotic grasses are also found.

Field methods

We selected pastures for sampling based on the presence of dry grasslands in hilltops and mesic grasslands in swales, as well as absence of exotic grasses. At each site, we counted birds in at least one homogeneous short grass pasture, one homogeneous tall grass pasture and one pasture of intermediate structure. Sampling was carried out in late December 2009-2010. We restricted sampling to the breeding season of the local avifauna (Belton 1994) to avoid bias. At this time of the year birds are more vocal and restricted to territories, favoring detection and minimizing chances of double-counting individuals (Bibby *et al*. 1992). Furthermore, late summer migrants, namely *Sporophila* seedeaters, are already present in grasslands in December (Belton 1994).

Birds were counted in 400 x 100 m plots. We allocated two plots per pasture, one on the hillcrest and another on an adjacent swale. Our sample consisted of 22 plots in dry grasslands and 22 plots in mesic grasslands. Plots were at least 300 m apart in order to minimize double-counting the same individuals and distant 200 m from the borders of pastures to minimize edge effects (Reese & Ratti 1988). We did not sample grasslands with trees or large aggregations of bushes. All distances were determined with a hand-held GPS with a 5 m error.

Bird counts were carried out by two observers walking at a constant rate along the center of the plot. Each observer screened a 50 m half section of the plot. All birds seen or heard were counted, except individuals in flight. When necessary, distances from the observer to individual birds were checked with a telemeter in order to ensure that only individuals inside the plot were counted. Counts were realized in the early morning or late afternoon in clear days with wind speed inferior to 5 on the Beaufort scale to minimize bias (Bibby *et al*. 1992; Ribic & Sample 2001).

We sampled a reduced number of habitat variables selected according to their importance to grassland birds (Fisher & Davis 2010), but ensured that the variability of habitats used by multiple species was contemplated (Wiens 1969). In each plot, we measured habitat variables in 16 points systematically allocated in pairs at 50 m intervals, totalizing 16 points per plot. The exact distance of each point to the central line of the plot was randomized. Since short-grass pastures were very homogeneous, we reduced the number of points to eight in these cases. In each point, we visually estimated the percentage of standing cover of grasses, forbs, shrubs (mainly *Baccharis* spp.), *Eryngium* spp., bare ground and water within a 1 m² sampling frame. We measured *Eryngium* spp. independently from other forbs because birds use the tall inflorescence of this plant as perching sites. We further distinguished the large, wet-soil *E. pandanifolium* from smaller species of this genus because some bird species are restricted to formations of this plant. We also estimated the total area covered by bushes in a given plot. We pooled all coverage measures to produce an estimate of each variable for the whole plot. We then calculated the Shannon-Wiener diversity index for all coverage variables in a given plot and used this value as a proxy for diversity of biotic and abiotic horizontal coverage in the analyses (see Tews *et al*. 2004 and Fisher & Davis 2010).

In each sampling point we additionally measured the height of the herbaceous vegetation at each corner of the sampling frame. We then calculated the mean value of all measurements in a plot and used this metric in the analyses. We measured the vertical density of the vegetation using visual obstruction readings at a Robel pole; we took four measurements 1 m aboveground in each corner of the sampling frame at a distance of 4 m from the pole (Robel *et al.* 1970). We then calculated a heterogeneity index based on these measurements to express the variability of vertical density according to the equation in Wiens (1974): H.I. = $\sum$ (max - min) / $\sum$means, where amplitudes of the four values at each point are summed and divided by the sum of the means of the four values in each point.

Statistical analyses

We explored association patterns of sampling units described by habitat variables (i.e., the eight biotic and abiotic horizontal coverage measures, mean vegetation height and

the variability of vertical density of the vegetation) using principal component analysis (PCA). Environmental variables were previously scaled by standardization.

We used randomization tests (Pillar & Orlóci 1996; Manly 2007) to test for differences in vegetation height and the variability of vertical density of the vegetation in both levels of topography (i.e., dry and mesic grasslands). Our null hypothesis was that there was no difference between these descriptors in both groups. We ran 10,000 iterations and set the alpha level to 0.05.

We also tested two sets of different models in order to evaluate the effects of topography, environmental variables and their interactions upon bird diversity. We used univariate linear models to evaluate species density (i.e., the number of species per plot) and multivariate linear models for community composition. Each set of analysis comprised four distinct models: model 1 is an ANCOVA and evaluates the effect of topography and its interaction with environmental variables, while adjusting species density means to what they would be if both levels of topography were equal on their covariate values; model 2 is a multiple regression, including topography and all environmental variables; model 3 is a multiple regression considering only the environmental variables; and model 4 is a simple regression model including only topography (Table 1).

Models were selected following an information-theoretic approach (Burnham & Anderson 2002, 2004; Johnson & Omland 2004). We used second order Akaike Information Criterion (AICc) to measure model plausibility for species density. We then calculated the delta AICc (ΔAICc) for each model, which is the relative difference in AICc values between each model and the top-ranked model, and the AICc weight (w), which is the relative likelihood of the model given the data, normalized across the set of candidate models to sum to one (Burnham & Anderson 2002, 2004; Johnson & Omland 2004). We repeated the same procedure to evaluate the effects of predictors on community composition, using multivariate linear models and Akaike Information Criterion (AIC) instead of AICc, as the modifications in the correction term in AICc do not apply for multivariate response data (but see Fujikoshi & Satoh (1997) for a modified AICc for multivariate data). We standardized (scaled to zero mean and unit variance) the environmental variables previously to analysis.

The PCA ordination was carried out in CANOCO 4.5 (ter Braak &Šmilauer 2002) statistical software. Randomization tests were performed on MULTIV 2.6.3b (Pillar 2007) statistical software. Model selection analyses were run in R (v2.15.1; R Development Core Team 2012) using the "stats" and "bbmle" libraries.

Results

The first two PCA axes accounted for nearly 40% of the variance in the relationships between plots and environmental variables (Fig. 1). Plots from mesic grasslands in swales exhibited greater proportion of water, bare ground (mostly mud), bush and *E. pandanifolium* cover. Dry grasslands in hilltops had larger coverage of grasses and *Eryngium* spp. other than *E. pandanifolium*. Vegetation was significantly higher in swales (mean = 46.22 cm; SD = 20.76) than in hilltops (mean = 25.32 cm; SD = 13.99) (p = 0.0005), whereas the vertical density of the vegetation was more variable in hilltops (mean = 1.06; SD = 0.29) than in swales (mean = 0.84; SD = 0.34) (p = 0.028).

We recorded 51 species of birds and 489 individuals in swales, and 31 species and 249 individuals in hilltops (Appendix I). Twenty-eight species were exclusive of swales, eight of hilltops, and 23 occurred in both topographic levels.

Habitat variables were better predictors of species density than topography, since the model that does not consider topography was the most plausible (Table 2). The summed model probabilities (wAICc) also demonstrate that habitat is more important than topography in determining the number of species in a given plot (summed probabilities: 1.0 vs. 0.39).

Species composition, on the other hand, was totally predicted by topography and its interactions with habitat variables. Model 1 alone was the only plausible explanation for variation in species composition (summed probability = 1).

Discussion

Our results demonstrate that habitat features and topography affect species density and composition in different ways. While the number of species in plots depended largely on the variability of habitat features, composition was entirely predicted by topography and underlying habitat variables.

The variability of habitat variables was a key determinant of the number of species in pastures irrespective of topography. Grassland bird diversity is largely determined by vegetation heterogeneity, especially variations in height and density of the herbaceous vegetation (Fisher & Davis 2010). In our study system, overgrazing and mowing are the main factors responsible for simplifying grassland habitat. Degraded pastures in both hilltops and swales tend to display a homogeneous cover of stunted herbs (although the vegetation is always comparably taller in the latter). Few species, mostly *Nothura maculosa*, *Vanellus chilensis* and pipits (*Anthus*), occur in these pastures. Tussocks, forbs, shrubs, bushes and other features that increase habitat diversity are lacking in overgrazed or mowed areas. Presence of these "keystone structures" increases faunal diversity in open-vegetation systems through the provision of resources, shelter or 'goods and services' that enable species which otherwise would be absent to persist (Tews *et al*. 2004).

As expected, the effect of topography upon bird diversity was related with the formation of determined habitat types, which in turn affect the composition of avian communities. In our study system, topography seems to interact with habitat features important for birds in two ways: (1) by enhancing spatial heterogeneity through keystone structures; and (2) by minimizing the degradation of grassland habitat features by high pressure livestock grazing and trampling.

Mud and water puddles are two keystone structures recorded solely in swales. These features enabled wetland species, namely ducks, waders, rails and snipes, to occur in a grassland region which otherwise would not have adequate habitat. Stands of plants found in swales also provided key habitat for some species. These plants usually display high dominance, growing in large tussocks and forming dense stands (Cingolani *et al*. 2003; Focht & Pillar 2003). The architecture of the vegetation and the humidity of the soil provide shelter, foraging substrate and nesting opportunities for a series of passerines that depend on dense herbaceous vegetation to complete their life cycles. This includes *Limnoctites rectirostris*, a passerine entirely restricted to *E. pandanifolium* formations and that displays special adaptations to live in the dense, spiny vegetation (Olson *et al*. 2005).

The presence of dense stands of spiny or unpalatable plants apparently reduces the grazing and trampling pressure by livestock in swales, enabling bushes and grasses,

including some species also found in hilltops, to develop. This attracts birds that depend on woody vegetation for perching or nesting, such as flycatchers, and provides refuge for tall-grass specialists sensible to habitat degradation. Among these are threatened grassland species, such as *Xolmis dominicanus*, *Xanthopsar flavus* and *Sporophila* seedeaters (Azpiroz *et al*. 2012). Furthermore, native grasses that produce small seeds (*Paspalum* spp. and *Echynochloa* sp.) important to gravinorous birds, such as the threatened *Sporophila* seedeaters (Bencke *et al*. 2003), and that are absent from overgrazed areas can seed among these plants, providing an important resource to birds.

Local cattle ranching management practices apparently are able to ensure conservation of grassland biodiversity, as long as pastures of distinct vegetation structure are available in the landscape context. The maintenance of tall tussock communities in swales is crucial, especially where hilltop grasslands are subject to intense grazing regimes.

Our study revealed that differences in relief position and associated variations in habitat features determine two distinct grassland bird communities in the *Campos* grasslands of southern Brazil. However, variations in habitat variables are more important than topographic position in determining species density in pastures. Consequently, poor livestock management leading to overgrazing and habitat simplification will result is loss of avian grassland diversity irrespective of the topographic position of pastures. Our results also indicate that grasslands in swales are important in maintaining vegetation features which tall-grass specialists, including threatened species, use, as well as some species which depend on wet habitats which otherwise would be absent from the landscape. This suggests that these grasslands indeed serve as refuges for species that are not able to survive in overgrazed situations. However, maintenance of overall diversity in our study system can only be achieved if both grassland types are conserved.

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Table 1. Specification of models used in species density and species composition analysis. Topography has two levels: hilltops and swales.

Model 1	y ~ topography*(cover + height + density)
Model 2	y ~ topography + cover + height + density
Model 3	y ~ height + cover + density
Model 4	y ~ topography

Cover: Shannon-Wiener diversity index for all biotic and abiotic coverage variables in a given plot

Height: mean height of the vegetation in a given plot

Density: index expressing the variability of vertical density of the vegetation in a given plot

Table 2. Model selection for species density. K = number of parameters. See Table 1 for model specification.

	AICc	K	ΔAICc	wAICc
Model 3	216.6	5	0	0.61
Model 2	218.7	6	2.1	0.21
Model 1	219.0	9	2.4	0.18
Model 4	243.5	3	27	0

Table 3. Model selection for species composition. K = number of parameters. See Table 1 for model specification.

	AIC	K	ΔAIC	wAIC
Model 1	6609.65	9	0	1
Model 2	6891.64	6	281.99	0
Model 3	6932.61	5	322.96	0
Model 4	7228.73	3	619.08	0
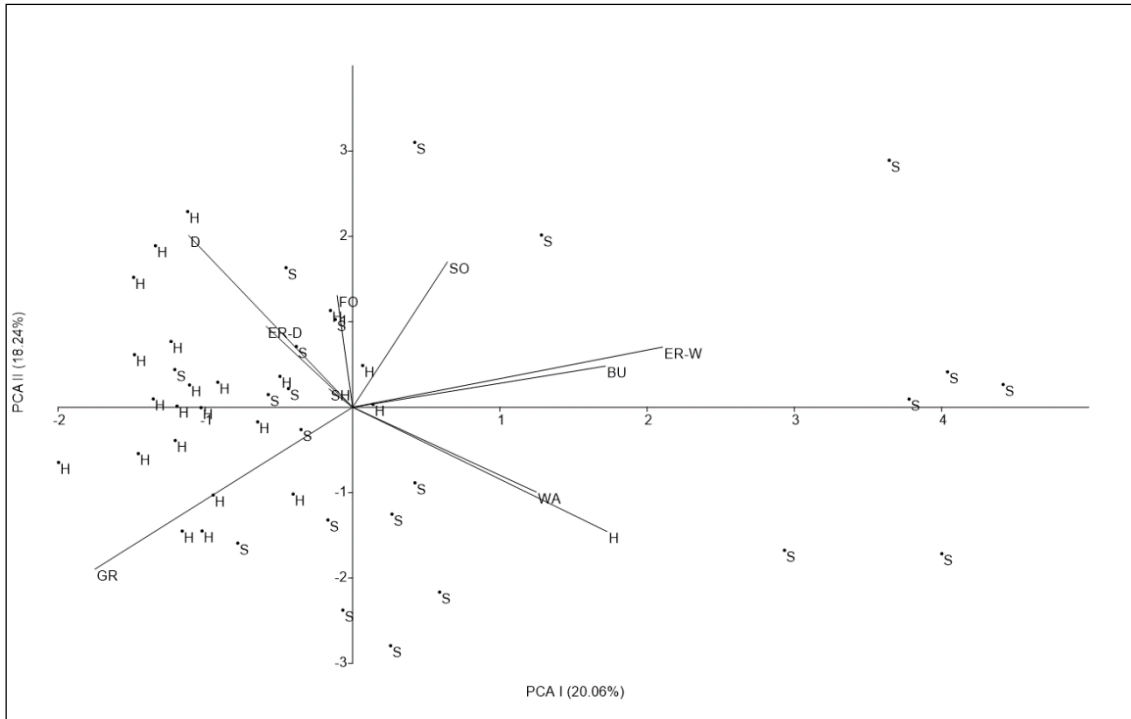
Figure 1. PCA ordination of sampling plots located in dry grasslands in hilltops (H) and mesic grasslands in swales (S) in relation to habitat features. GR – grass cover; FO – forb cover; SH – shrub cover; BU – bush cover; ER-W – *Eryngium pandanifolium* cover; ER-D – other species of *Eryngium* cover; WA – water cover; SO – bare ground cover; H – mean height of the vegetation; D – vertical density of the vegetation.

Appendix I. Abundance of bird species recorded in swale and hilltop grasslands in southern Rio Grande do Sul Brazil. The asterisk denotes global (IUCN 2011) conservation concern species.

	Hilltop	Swale
Nothura maculosa	12	8
Rhynchotus rufescens	2	3
Amazonetta brasiliensis	0	2
Bubulcus ibis	4	0
Butorides striatus	0	1
Plegadis chihi	0	1
Theristicus caudatus	6	0
Milvago chimango	2	0

Pardirallus sanguinolentus	0	2
Laterallus leucopyrrhus	0	2
Venellus chilensis	19	8
Gallinago paraguaiae	0	6
Bartramia longicauda	2	0
Athene cunicularia	0	1
Chlorostilbon lucidus	0	1
Hylocharis chrysura	0	1
Colaptes campestris	2	0
Furnarius rufus	0	17
Schoeniophylax phryganophila	0	4
Phacellodomus striaticollis	0	15
Limnoctites rectirostris	0	14
Anumbius annumbi	9	14
Thamnophilus ruficapillus	0	2
Elaenia obscura	0	1
Serpophaga nigricans	0	2
Myiophobus fasciatus	0	3
Pyrocephalus rubinus	1	0
Satrapa icterophrys	1	1
Machetornis rixosus	2	2
Tyrannus melancholicus	1	0
Tyrannus savana	7	16
Pitangus sulphuratus	2	5
Knipolegus lophotes	2	0
*Xolmis dominicanus**	0	3
Anthus furcatus	4	1
Anthus hellmayri	41	19
Cistothorus platensis	7	22
Mimus saturninus	1	7
Turdus rufiventris	0	1

Zonotrichia capensis	10	40
Ammodramus humeralis	32	36
Donacospiza albifrons	10	12
Poospiza nigrorufa	0	6
Sicalis flaveola	0	5
Sicalis luteola	42	72
Emberizoides herbicola	2	5
Emberizoides ypiranganus	0	2
Embernagra platensis	6	47
Volatinia jacarina	8	4
Sporophila caerulescens	0	4
*Sporophila cinnamomea**	2	16
Paroaria coronata	0	2
Geothlypis aequinoctialis	0	7
Pseudoleistes virescens	0	6
*Xanthopsar flavus**	0	27
Sturnella superciliaris	0	3
Agelaioides badius	4	3
Molothrus rufoaxillaris	2	4
Molothrus bonariensis	4	3

CAPÍTULO 3

SHIFTS IN COMPOSITION OF AVIAN COMMUNITIES RELATED TO TEMPERATE-GRASSLAND AFFORESTATION IN SOUTHEASTERN SOUTH AMERICA

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ABSTRACT. Afforestation of temperate grasslands with fast-growing trees for industrial pulpwood production is spreading in South America. Despite high afforestation rates resulting from governmental policies that stimulate pulpwood production in grasslands of southern Brazil and Uruguay, the impact of this activity on biodiversity remains to be properly assessed. We used an Impact-Reference study design to evaluate how grassland afforestation affects the composition of grassland bird assemblages. We sampled eucalyptus plantations and neighboring natural grasslands in southern Brazil from 2006–2009, and relied on nested sampling and analysis to separate the effects of afforestation from the natural variability of grasslands. We recorded a significant difference in composition between assemblages from grasslands and tree plantations. Species adapted to open, treeless areas tended to be negatively affected in relation to edge or forest birds in eucalyptus plantations. Afforestation is systematically replacing the bird assemblage of hilltop grasslands by a collection of common edge and forest species that occur in nearby riverine and hillside forests. Although most grassland birds negatively affected by tree plantations are common and widespread, observed and predicted afforestation rates in southeastern South America may result in regional population reductions in the near future.

KEYWORDS. Río de la Plata Grasslands, pulpwood, environmental impact, Impact-Reference, eucalyptus, Brazil.

RESUMO. **Alterações na composição de comunidades de aves relacionadas ao florestamento de campos temperados no sudeste da América do Sul**. O florestamento de campos temperados com árvores de crescimento rápido para a produção industrial de celulose está aumentando na América do Sul. Apesar das elevadas taxas de florestamento resultantes de políticas governamentais que estimulam o plantio de árvores para celulose em campos do sul do Brasil e Uruguai, o impacto dessa atividade sobre a biodiversidade ainda carece de avaliação adequada. Utilizamos um delineamento experimental do tipo impacto-referência para avaliar como o florestamento dos campos afeta a composição da assembleia de aves campestres. Amostramos plantações de eucalipto e campos nativos no sul do Brasil entre 2006–2009 e nos valemos de amostragem e análise aninhada para separar os

efeitos do florestamento da variabilidade natural dos campos. Registramos uma diferença significativa na composição entre as assembleias de aves do campo e de plantações de eucalipto. Espécies adaptadas a áreas abertas destituídas de árvores foram afetadas negativamente pelo florestamento, ao passo que aves florestais ou de borda de floresta foram favorecidas pela plantação de eucalipto. O florestamento está sistematicamente substituindo a assembleia de aves de campos de topos de morros por uma coleção de espécies de floresta e de borda comuns em matas ciliares e de encosta. Apesar de a maioria das espécies campestres afetadas negativamente pelas plantações de árvores serem comuns e de ampla distribuição, as taxas de florestamento observadas e previstas no sudeste da América do Sul podem gerar reduções populacionais regionais num futuro próximo.

PALAVRAS-CHAVE. Campos do Rio da Prata, celulose, impacto ambiental, Impacto-Referência, eucalipto, Brasil.

INTRODUCTION

Habitat loss and degradation are the main drivers of biodiversity loss (GROOM & VYNNE, 2006). These factors affect biodiversity via the elimination, displacement or modification of populations of native and invasive species, altering the structure of communities and ecosystems (GROOM & VYNNE, 2006). Since habitat loss usually reduces niche availability, ecologically specialized taxa with narrow niche requirements are expected to be at greater risk of extinction than generalists (OWENS & BENNETT, 2000; BUTLER *et al.*, 2007). Traits shared by species that are negatively affected by habitat loss, degradation and fragmentation include low mobility, low fecundity and recruitment, and narrow niche requirements, whereas well-distributed invasive taxa and habitat-generalists are usually listed as winners in altered landscapes (BEISSINGER, 2000; GROOM & VYNNE, 2006; NOSS *et al.*, 2006).

Habitat loss and degradation have been severe in temperate grasslands, especially in the vast Río de la Plata Grasslands of southeastern South America, which have lost nearly 60% of the original cover (SORIANO *et al.*, 1992; HENWOOD, 2010; AZPIROZ *et al.*, 2012). The remaining grasslands are located mostly in the northern part of the region, especially in the *campos* unit of northeastern Argentina, Uruguay and southern Brazil

(V{\sc ega} *et al.*, 2009). Traditionally used for livestock grazing, an activity compatible with conservation if properly managed (D{\sc eveley} *et al.*, 2008; C{\sc astilhos} *et al.*, 2009), the *campos* are currently under assault from the expansion of agriculture and commercial forestry (O{\sc verbeck} *et al.*, 2007; V{\sc ega} *et al.*, 2009). Only 0.2% of the *campos* are protected (H{\sc enwood}, 2010), an alarming situation considering that these grasslands are highly biodiverse and harbor many threatened and endemic taxa (O{\sc verbeck} *et al.*, 2007; B{\sc encke}, 2009; B{\sc oldrini}, 2009; A{\sc zpiroz} *et al.*, 2012).

Small groves of eucalyptus and pines planted for shade and lumber have been a common feature in the *campos* since the mid-XIXth century (H{\sc asse}, 2006). Large-scale afforestation began in the 1980s, when large pulpwood companies were attracted to the region by governmental tax benefits and financial subsidies (C{\sc arrere} & L{\sc ohmann}, 1996; H{\sc asse}, 2006; V{\sc ihervaara} *et al.*, 2012). In Uruguay and southern Brazil, where land officially offered for afforestation coincided with grassland remnants, environmental licensing processes were controversial and embedded in ideological disputes (C{\sc arrere} & L{\sc ohmann}, 1996; H{\sc asse}, 2006; G{\sc autreau} & V{\sc élez}, 2011). Currently, tree plantations cover approximately 1,120,000 ha in the *campos* of Uruguay and the Brazilian state of Rio Grande do Sul (G{\sc autreau} & V{\sc élez}, 2011).

Plantation forests can be of conservation value in deforested regions, especially when managed to promote stand structural complexity and landscape heterogeneity that benefit forest organisms suffering from habitat loss, edge effects and connectivity breakdown (B{\sc rockerhoff} *et al.*, 2008). In natural grassland areas, however, afforestation is detrimental (B{\sc rockerhoff} *et al.*, 2008). Major biotic impacts on afforested grasslands are changes in abundance, diversity and composition of species assemblages in response to alterations in environmental conditions and disruption of ecological processes (A{\sc llan} *et al.*, 1997; C{\sc orley} *et al.*, 2006; B{\sc uscardo} *et al.*, 2008; L{\sc antschner} *et al.*, 2008; B{\sc erthrong} *et al.*, 2009).

Despite the increase in the number and extent of commercial tree plantations in South America, the impact of this activity on grassland biodiversity remains to be properly assessed. Our main goal was to evaluate how afforestation affects the composition of grassland bird assemblages. We proposed that afforestation has a press (sustained) impact (*sensu* B{\sc ender} *et al.*, 1984) on grassland faunal assemblages. Consequently, we predicted that bird assemblages in grasslands and tree plantations

would be structurally different. We also expected that species that are strictly adapted to grassland habitats would be negatively affected in relation to forest and edge birds. Our sampling design and analytical procedures were devised to disentangle the effects of afforestation from natural variability, allowing us to adequately measure anthropogenic impact. This is the first study to use this approach to quantify changes in faunal assemblages following temperate-grassland afforestation.

MATERIAL AND METHODS

Study area. Our study area spanned 4,918 km^2 in southern Rio Grande do Sul, Brazil's southernmost state (Table 1). Most of our sites are located in the *Planalto Sul-Rio-Grandense*, an upland system of eroded granite hills, with a few located in the gently rolling terrain of the neighboring *Depressão Central* sedimentary region (IBGE, 1986). Climate is subhumid; mean annual temperature and precipitation in the region are 16–18°C and 1,200–1,400 mm, respectively (IBGE, 1986).

In this region, grasslands predominate on flat or gently rolling terrain (IBGE, 1986; OVERBECK *et al.*, 2007). Natural forest occurs mostly in valleys, especially in the northeastern sector of our study area (IBGE, 1986). Gallery forests occur along most watercourses, and marshes cover floodplains and swales (IBGE, 1986). Herbaceous and shrubby vegetation predominates in grasslands, with Poaceae, Asteraceae, Rubiaceae and Leguminosae being the main families (BOLDRINI, 2009). Scattered trees and bushes are common in the *Planalto Sul-Rio-Grandense* grasslands. Cattle, sheep and horse ranching are the main economic activity.

The eucalyptus plantations sampled for this study were established in 2004–2006. Eucalyptus trees were planted in hilltop grasslands hitherto used for cattle grazing. Moister grasslands in swales and drainages were not afforested, in accordance with Brazilian environmental law. Stands were of different sizes, limited by roads and watercourses. The Sydney blue gum *Eucalyptus saligna* Smith (Myrtaceae) and the flooded gum *Eucalyptus grandis* Hill ex Maiden (Myrtaceae) were the main species cultivated. Plants were spaced 3.0 x 2.0 m apart. Herbicides and insecticides were applied in the first year. After seven years, trees are cut and new saplings planted.

Experimental design. Since the plantations were established before we had access to the area, we used an Impact-Reference study design (*sensu* WIENS & PARKER, 1995). In this scheme, samples are taken at a single time within the impacted area, and from nearby areas that were not impacted and constitute references (WIENS & PARKER, 1995). Despite being less powerful and having reduced causal inference ability when compared to BACI or Beyond-BACI designs that rely on 'before and after impact' information (UNDERWOOD, 1994; WIENS & PARKER, 1995), post-impact tests have been widely used to assess differences between impact and reference sites (see BENEDETTI-CECCHI & OSIO, 2007).

The plantations covered a broad area, enabling us to rely on nested sampling design and analysis (*sensu* UNDERWOOD, 1997) to separate the effects of afforestation from natural variability in reference areas. This peculiar spatial distribution also relieved us from using an asymmetrical analysis to avoid pseudoreplication (UNDERWOOD, 1994; GLASBY, 1997).

Our design consisted of two treatments (afforestation and grassland) replicated at 11 sites. At each site we allocated five 500 x 100 m plots per treatment, and counted birds in them. Our sample consisted of 55 impact plots from eucalyptus stands, and 55 reference plots from grasslands.

We only sampled natural hilltop grasslands used for livestock grazing, avoiding pastures planted with exotic grasses. All eucalyptus stands were 2–3 years old with trees 4–6 m tall. We used a systematic sampling design, choosing the location of the first plot on a map and determining the starting point of subsequent plots at 700-m intervals to ensure independence (HURLBERT, 1984). On many occasions, however, this distance was altered to ensure that plots lay fully within a fenced grassland section or eucalyptus stand. When this occurred, a minimum distance of 200 m between plots was always respected. Grassland plots were at least 200 m from the nearest eucalyptus stand and natural forest patches. Distances were determined with a hand-held GPS with a 5-m error.

Bird sampling. Sampling was carried out from 2006–2009 (Table 1). To conform to the premises of the study design and avoid detection bias, we sampled each site only once, in November-December, the peak of the breeding season of the local avifauna (BELTON, 1994). Birds are vocal and restricted to their territories during this period, favoring

detection and minimizing chances of double-counting individuals (Bɪʙʙʏ *et al*., 1992). Counts were carried out by two observers walking at a constant speed along the central line of the plot. Each observer was responsible for searching a 500 x 50 m half-section of the plot. We counted all birds that were seen or heard. Individuals in flight were omitted. To favor detection, counts were made in the early morning or late afternoon, in good weather conditions (Bɪʙʙʏ *et al*., 1992).

Habitat use of birds was defined according to Bᴇʟᴛᴏɴ (1994) and Vɪᴄᴋᴇʀʏ *et al*. (1999). Threat categories followed IUCN (2011) and scientific nomenclature followed Rᴇᴍsᴇɴ *et al*. (2011).

Statistical analyses. We employed permutational analysis of variance using the pseudo F-ratio as test criterion (Pɪʟʟᴀʀ & Oʀʟóᴄɪ, 1996; Aɴᴅᴇʀsᴏɴ, 2001) to evaluate if differences in the composition of bird assemblages between treatments were significant. We used the Bray-Curtis distance between sampling units. Our null hypothesis was that there was no difference in composition between impact and reference areas. Our nested design allowed us to partition the total variation within three factors: among treatments, among sites and among plots. Since our main interest was to understand the effect of afforestation, we blocked both nested factors (sites and plots) to remove the effect of spatial variability from our treatments. We then divided the total sum of squares by the sum of squares between treatments, to determine the proportion of variation explained exclusively by treatments. In both tests we ran 10,000 iterations and adopted an alpha level of 0.05 to consider differences significant.

To determine species positively and negatively affected by grassland afforestation, we relied on a classification method developed to determine habitat specialists and generalists (Cʜᴀᴢᴅᴏɴ *et al*., 2011). This method uses a multinomial model based on estimated species relative abundance in two habitats, to classify species into four categories: (1) generalists, (2) specialists of habitat "a", (3) specialists of habitat "b", and (4) species too rare to classify (Cʜᴀᴢᴅᴏɴ *et al*., 2011). Major advantages of this method include the classification of habitat specialists and generalists without the a priori exclusion of rare species, and the capability of distinguishing habitat generalists (species with no significant habitat affinity) from species that are simply too rare to classify (Cʜᴀᴢᴅᴏɴ *et al*., 2011). Following recommendations by Cʜᴀᴢᴅᴏɴ *et al*. (2011),

we set the specialization threshold *K* to 0.667 and the *P* level to 0.005. We assumed that species classified as grassland specialists would be negatively affected by afforestation, whereas eucalyptus specialists would be favored.

Classification of specialist and generalist species was performed on CLAM (CHAO & LIN, 2011), whereas permutational analyses of variance were carried out on MULTIV 2.63 statistical software (PILLAR, 2007).

RESULTS

We recorded 994 individuals and 57 species in grasslands, and 442 individuals and 54 species in eucalyptus stands. Thirty species were shared between treatments, 27 were recorded solely in grasslands, and 24 occurred only in afforestation stands (Table 2). The difference in composition between assemblages was significant (*p* = 0.0001), with afforestation explaining 22% of the total variation.

Of the 81 species recorded in both treatments, nine were considered grassland specialists (species negatively affected), six were eucalyptus afforestation specialists (species positively affected) and 13 were generalists (Table 2). Approximately 65% of the species were too rare to classify. Among grassland specialists, six species were recorded solely in grasslands. Three afforestation specialists were detected only in eucalyptus stands. Roughly half of the 40 grassland obligate and facultative birds were absent from eucalyptus plantations (Table 2).

Xolmis dominicanus (Vieillot, 1823), listed as vulnerable, was the only threatened species recorded. *Rhea Americana* (Linnaeus, 1758) and *Cyanocorax caeruleus* (Vieillot, 1818) are considered "near-threatened".

DISCUSSION

Our results indicate that the bird assemblages inhabiting grasslands and eucalyptus stands differed in species composition. Although we did not use 'before data', our robust sampling design and use of randomization tests enabled us to determine how much of the variation in composition between impact and reference areas was explained by natural variability and/or differences in treatments.

Differences in composition between biotic assemblages of afforested and open areas are a characteristic feature of natural and anthropogenic afforestation in natural and man-made grasslands (CLAVIJO *et al*, 2005; LANTSCHNER *et al*., 2008). Compositional alterations in faunal assemblages reflect changes in vegetation structure, spatial distribution, and composition of plant communities that occur during the afforestation process (SAMWAYS*et al*., 1996; LACHANCE & LAVOIE, 2005; CORLEY *et al*., 2006; LANTSCHNER *et al*., 2008).

Grassland specialists – the species negatively affected by afforestation in our study system – include five grassland obligate and three grassland facultative species (*sensu* VICKERY *et al*., 1999). Another three grassland obligate species and four grassland facultative species were considered generalists, suggesting that they may be somewhat tolerant to afforestation (but see below). A grassland obligate, *Rhynchotus rufescens* (Temminck, 1815), and a grassland facultative, *Zonotrichia capensis* (Statius Muller, 1776), were considered afforestation specialists. At least in part this paradox is explained by the fact that sampling was done in the early stages of afforestation, when trees were not fully developed and small patches of grassland vegetation were still found in the stands, especially in sectors where eucalyptus saplings had died. Grassland birds recorded in eucalyptus stands were found mostly in these grassy remnants. The absence of livestock enabled grasses to grow tall in the stands, allowing grassland birds adapted to live in dense vegetation, such as *R. rufescens* and *Embernagra platensis* (Gmelin, 1789), to linger in these areas. These species are naturally rare in adjacent heavily grazed hilltop grasslands, being normally restricted to the denser swales. Furthermore, open-habitat taxa that use shrubby or arboreal vegetation for perching or nesting, such as some pigeons, ovenbirds, sparrows and finches, were also able to persist in eucalyptus stands because of the small size of the trees. We expect that most grassland birds observed in the eucalyptus stands will disappear as the fast-growing trees fully develop and grassland remnants become shaded.

Most grassland species, including all obligate and facultative taxa classified as grassland specialists, are common and widespread in the Río de la Plata Grasslands and other South American open-vegetation ecosystems (MATA *et al*., 2006; RIDGELY & TUDOR, 2009). Despite their abundance and wide distribution, observed and predicted

rates of grassland conversion in the region (HASSE, 2006; GAUTREAU & VÉLEZ, 2011; VIHERVAARA *et al.*, 2012) suggest that afforestation may represent a threat at a regional scale to some of these species in the near future. At least for the threatened *X. dominicanus*, which depends on hilltop grasslands for foraging (BENCKE, 2009), tree plantations may already be an important impact. Furthermore, the overall similarity of the southern Brazilian and Uruguayan grassland avifaunas (BELTON, 1994; MATA *et al.*, 2006; RIDGELY & TUDOR, 2009) indicates that afforestation is likely to impact birds in a similar way throughout the entire *campos* region.

Our results also indicate that direct habitat loss resulting from afforestation has a smaller impact on threatened grassland birds than on common species. Eleven threatened grassland birds occur in the *campos* of southern Brazil and Uruguay (IUCN, 2011; AZPIROZ*et al.*, 2012). Alongside *X. dominicanus*, two other globally threatened grassland birds occur in our study region: *Sporophila cinnamomea* (Lafresnaye, 1839) and *Xanthopsar flavus* (Gmelin, 1788). The latter two were observed solely in wet grasslands located in swales, which explains their absence from our hilltop samples. However, indirect effects of afforestation, such as water consumption and shading, are expected to impact wet grasslands and jeopardize the survival of threatened grassland birds within tree plantations, even though swales are not cultivated (see below).

Roughly 60% of the 103,000 ha of land acquired for afforestation in our study area was not converted, in accordance with Brazilian environmental law (which protects some landscape features and a proportion of the natural vegetation), and because natural barriers such as rocky outcrops and pronounced slopes hindered cultivation. Some of these areas were rented for cattle ranching, but most remained unused. While riverine and hillside forests cover the largest portions, wet grasslands and marshes important for threatened grassland birds predominate in some swales and floodplains, especially in the southern and western sectors of our study region. The existence of these large amounts of natural vegetation within plantations was widely used as environmental propaganda by the pulpwood industry, which merchandised them as 'conservation' areas. Recent studies have shown that the conservation value of these 'ecological networks' for grassland species is greatly limited, mostly because of habitat unsuitability (LIPSEY & HOCKEY, 2010) and high rates of nest predation (REINO *et al.*, 2010).

Most species positively affected by afforestation and some generalists are edge or forest birds. Forest and edge birds also predominated among the species recorded solely in eucalyptus stands, including those listed in the 'too rare to classify' category. Some of these, such as *Pachyramphus polychopterus* (Vieillot, 1818), *C. caeruleus* and *Basileuterus leucoblepharus* (Vieillot, 1817), are strongly associated with forests in our study area and seldom observed in open vegetation. LANTSCHNER *et al*. (2008) also observed that afforestation in Patagonian grasslands tended to benefit woodland birds more than open-vegetation taxa. The diversity of organisms favored by afforestation in tree plantations depends largely on landscape heterogeneity and stand complexity (LINDENMAYER & HOBBS, 2004; BROCKERHOFF *et al*., 2008). Plantations in our study area are comprised by non-flowering clone plants, and are managed to prevent the development of understory vegetation. Therefore, two key features that augment bird diversity in Brazilian eucalyptus plantations (WILLIS, 2003) are lacking. Forest cover is naturally restricted in our study area, further limiting the species pool able to colonize eucalyptus stands. Indeed, the majority of forest species that we recorded are common inhabitants of various forest types in southern Brazil (BELTON, 1994). Most birds that we recorded in eucalyptus stands appeared to be foraging or moving through the plantations. We frequently observed individuals of *Z. capensis*, *Turdus amaurochalinus* Cabanis, 1850, *Leptotila verreauxi* Bonaparte, 1855, *Turdus rufiventris* Vieillot, 1818, *Lathrotriccus euleri* (Cabanis, 1868), and *P. polychopterus* singing in eucalyptus stands, which is an evidence of territoriality. *Zonotrichia capensis* was recorded nesting in grasses below eucalyptus trees, while nests of *Turdus* spp. and of an unidentified dove (probably *L. verreauxi*) were observed in some eucalyptus trees. We expect the proportion of forest and edge birds nesting in eucalyptus stands to increase as the trees develop.

We demonstrated that the main impact of temperate grassland afforestation on faunal assemblages is the change in composition resulting from the replacement of grassland organisms by edge and forest taxa. Although most grassland birds are common and widespread, the observed and predicted conversion rates in the *campos* of Brazil and Uruguay may represent an important threat to regional populations of some of these birds in the near future. At least one threatened species may already be experiencing population loss resulting from afforestation in our study area. Species

benefiting from afforestation are common edge and forest birds throughout the region. Since plantations are managed solely for pulpwood production on very short rotation periods, habitat features that could further benefit these species are absent, decreasing the conservation value of afforested areas. Urgent awareness and action is needed to prevent further loss of temperate grasslands to afforestation in southeastern South America.

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Table 1. Characteristics of sites sampled in southern Brazil.

Site	Municipality	Coordinates	Altitude (m)	Geo [a]	Sampling date
Fazenda Seival	Candiota	31°21'11''S, 53°42'53''W	315	DC	Dec 2007
Fazenda Silveiras	Pinheiro Machado	31°31'34''S, 53°33'22''W	255	PSRG/DC	Dec 2008
Fazenda São José	Pinheiro Machado	31°35'30''S, 53°33'51''W	280	PSRG/DC	Dec 2007
Fazenda da Ferraria	Piratini	31°43'18''S, 53°00'34''W	130	PSRG	Dec 2006
Fazenda Nossa Senhora de Guadalupe	Capão do Leão	31°47'16''S, 52°39'08''W	85	PSRG	Nov 2007
Fazenda Santa Heloísa	Pedras Altas	31°49'38''S, 53°35'59''W	300	PSRG	Dec 2007
Fazenda São Francisco	Pedras Altas	31°54'47''S, 53°37'08''W	200	PSRG	Dec 2006
Fazenda do Bote	Herval	32°03'10''S, 53°30'41''W	230	PSRG	Dec 2006
Fazenda Recanto dos Paz	Arroio Grande	32°07'15''S, 52°55'46''W	50	PSRG	Dec 2008
Fazenda do Banheiro	Arroio Grande	32°15'34''S, 53°12'29''W	75	PSRG	Nov 2007
Fazenda Nova II	Jaguarão	32°22'45''S, 53°19'36''W	85	PSRG	Dec 2008

[a] Geo – geomorphologic unit (*sensu* IBGE, 1986). DC – *Depressão Central* sedimentary region. PSRG – *Planalto Sul-Rio-Grandense* uplands.

Table 2. Classification of bird species recorded in southern Brazilian grasslands and eucalyptus afforestation stands in four categories based on their estimated relative abundance in both treatments. The total abundance of each species in both treatments is given. A single asterisk denotes obligate grassland birds, while two asterisks indicate facultative grassland birds (*sensu* VICKERY*et al.*, 1999).

Category	Scientific name	Grassland	Eucalyptus
Grassland specialists	*Sicalis luteola**	89	0
	*Tyrannus savana**	80	7
	*Pseudoleistes virescens***	68	0
	*Vanellus chilensis**	58	0
	*Molothrus bonariensis***	57	0
	*Anthus hellmayri**	55	1
	*Geositta cunicularia**	21	0
	Sicalis flaveola	21	1
	*Colaptes campestris***	19	0
Afforestation specialists	*Zonotrichia capensis***	82	134
	Leptotila verreauxi	0	14
	Guira guira	2	13
	Turdus rufiventris	0	13
	*Rhynchotus rufescens**	2	12
	Vireo olivaceus	0	10
Generalists	*Nothura maculosa**	38	16
	Turdus amaurochalinus	34	47
	*Ammodramus humeralis**	31	6
	*Furnarius rufus***	29	15
	*Anumbius annumbi***	26	7
	Mimus saturninus	24	4
	*Zenaida auriculata***	21	8
	*Embernagra platensis**	16	4
	Tyrannus melancholicus	14	6
	*Agelaioides badius***	11	6

	Pitangus sulphuratus	10	12
	Elaenia parvirostris	9	20
	Troglodytes aedon	4	8
Too rare to classify	*Xolmis cinereus***	13	0
	*Columbina talpacoti***	12	4
	*Athene cunicularia**	12	0
	*Myiopsitta monachus***	11	0
	*Xolmis dominicanus***	11	0
	*Anthus furcatus**	11	0
	*Pseudoleistes guirahuro**	11	0
	*Sturnella superciliaris**	11	0
	*Rhea americana***	8	0
	Patagioaenas picazuro	8	1
	*Xolmis irupero***	8	0
	Pyrocephalus rubinus	5	1
	Pipraeidea bonariensis	5	0
	*Donacospiza albifrons***	5	2
	Colaptes melanochloros	4	0
	*Gnorimopsar chopi***	4	0
	*Bubulcus ibis***	3	0
	*Milvago chimango***	3	0
	*Columbina picui***	3	7
	Satrapa icterophrys	3	0
	*Machetornis rixosa***	3	0
	Paroaria coronata	3	2
	Saltator aurantiirostris	3	1
	*Molothrus rufoaxillaris***	3	0
	Knipolegus lophotes	2	0
	Geothlypis aequinoctialis	2	1
	*Caracara plancus***	1	0
	Phacellodomus striaticollis	1	0

Camptostoma obsoletum	1	2
Thraupis sayaca	1	0
Poospiza nigrorufa**	1	4
Sporophila caerulescens**	1	4
Pyrrhura frontalis	0	2
Tapera naevia**	0	2
Hydropsalis torquata**	0	2
Hylocharis chrysura	0	1
Thamnophillus ruficapillus	0	2
Serpophaga subcristata	0	4
Phylloscartes ventralis	0	1
Myiophobus fasciatus	0	3
Lathrotriccus euleri	0	6
Myiodynastes maculatus	0	1
Myiarchus swainsoni	0	3
Pachyramphus polychopterus	0	2
Cyclarhis gujanensis	0	1
Cyanocorax caeruleus	0	2
Coereba flaveola	0	1
Volatinia jacarina**	0	2
Coryphospingus cucullatus	0	6
Parula pitiayumi	0	1
Basileuterus culicivorus	0	1
Basileuterus leucoblepharus	0	1
Sporagra magellanica	0	5

CONSIDERAÇÕES FINAIS

Na presente tese versei sobre como distintas variáveis de habitat afetam a estrutura das comunidades de aves em campos temperados do sudeste da América do Sul, relacionando tais variações ao manejo das pastagens para pecuária e a perda de habitat para silvicultura. Teorias relacionadas ao uso diferencial do habitat por grupos de espécies e as formas como esses grupos são afetados pela degradação e perda de habitat interligam os capítulos. Os resultados de cada capítulo são complementares, permitindo compreender como essas atividades humanas afetam a diversidade de aves em campos e possibilitando a implementação de soluções práticas de manejo e conservação.

No primeiro capítulo demonstramos como distintos subgrupos de espécies utilizam os campos litorâneos de acordo com variações na arquitetura da vegetação herbácea e a presença de estruturas-chave, como plantas lenhosas. Visto que o pastejo e o manejo da pecuária são os principais determinantes da estrutura da vegetação, os impactos decorrentes da degradação de habitat pela criação extensiva de gado em campo nativo afetam os subgrupos de forma diferenciada. Aves restritas a campos de vegetação alta e densa são negativamente afetadas, ao passo que aves de campos ralos são favorecidas. A persistência de aves de capim alto na paisagem somente é possível porque densos estandes de espécies de plantas entouceiradas se mantêm em refúgios em depressões do terreno. Arvoretas isoladas e pequenas manchas de cactos existentes em alguns setores desses campos constituem as principais estruturas-chave (*sensu* Tews *at al*., 2004). Tais estruturas são responsáveis por ofertar recursos como substrato de pouso, cobertura para descanso e sítios de nidificação para uma série de espécies incapazes de cumprir todas as etapas de seu ciclo de vida exclusivamente na vegetação herbácea. Embora a criação de gado tenha promovido a diversidade regional ao criar manchas de diferentes alturas da vegetação na paisagem, o manejo em geral é direcionado à manutenção de vegetação rasteira, espacialmente homogênea nos potreiros, o que pode resultar na eliminação de um subgrupo inteiro de aves. Isso poderá resultar em extinções locais e redução da diversidade. Assim, recomendamos que o manejo mude de modo a assegurar a manutenção de grandes manchas de vegetação alta e densa nos potreiros, seja através de rotação de

pastagens ou pela exclusão de gado em algumas áreas, promovendo a ocorrência de vegetação densa e entouceirada.

Visto que grupos distintos de aves segregam-se de acordo com o porte da vegetação herbácea nos campos, investigamos, no segundo capitulo, de que forma variações no relevo interagem com variáveis de habitat e afetam a diversidade de aves na Campanha gaúcha. Também tínhamos interesse em avaliar se as manchas de vegetação herbácea alta e densa que persistem em depressões ao longo das linhas de drenagem poderiam servir de refúgio para aves dependentes de vegetação alta em áreas utilizadas para pecuária. Nesse sentido, utilizamos uma abordagem de seleção de modelos para compreender o papel do habitat, do relevo e suas interações sobre o número de espécies e a composição das comunidades de aves. Como esperado, as depressões possuem vegetação mais alta e homogênea quando comparadas aos campos mais secos dos topos de morros adjacentes. Essas feições também ostentam uma série de estruturas-chave, como água e arbustos, que não ocorrem em campos de topo de morro.

Nosso principal resultado foi demonstrar que a densidade de espécies de aves nos campos não tem nenhuma relação com o relevo, sendo inteiramente explicado por variações de habitat. Por outro lado, a interação entre o habitat e o relevo constituiu a única explicação para variações na composição das comunidades. Os principais fatores responsáveis por gerar as diferenças que observamos na composição referem-se à presença de estruturas-chave nas depressões, que possibilitam que aves aquáticas e Passeriformes que dependem de vegetação lenhosa ocorram em áreas dominadas por plantas herbáceas. A presença de grandes manchas de gravatás nessas áreas também oferece refúgio às aves, além de permitir que pequenas plantas vicejem livres do pastejo e pisoteio do gado, fornecendo recursos como sementes às aves granívoras.

Em termos práticos, nosso estudo demonstrou que as baixadas de fato constituem refúgios para as aves de vegetação alta, incluindo espécies ameaçadas. Também concluímos que o sobrepastejo ou técnicas de manejo que degradem e simplifiquem a vegetação campestre irão resultar em perda de diversidade de aves, independentemente da posição do potreiro na topografia. Visto que o relevo e as diferenças nas variáveis de habitat a ele associadas determinam diferenças na

composição, é necessário manejar e conservar baixadas e topos de coxilhas de forma independente, a fim de assegurar a manutenção da diversidade nessa região.

Por fim, demonstramos no último capítulo que o principal impacto da perda de habitat campestre decorrente da expansão da silvicultura é a substituição de uma série de espécies de aves essencialmente campestres, que são incapazes de sobreviver em meio às plantações de árvores, por uma coleção de espécies generalistas de borda e interior de floresta. Embora as espécies campestres que estão sendo afetadas pela perda de habitat sejam comuns e de ampla distribuição, as taxas observadas e previstas de conversão de campos em plantações industriais de árvores poderão resultar em declínios populacionais regionais importantes num futuro próximo. Nesse sentido, impedir que novas áreas de campo nativo sejam convertidas em talhões de árvores passa a ser imperativo.

Em suma, demonstramos que a degradação de habitat decorrente do manejo de gado em campo nativo afeta a comunidade de aves de forma diferencial. Aves adaptadas a campos ralos ou generalistas tendem a ser beneficiadas, ao passo que as espécies associadas à vegetação alta e densa são desfavorecidas. Também demonstramos que variações na topografia são responsáveis por reduzir os impactos da degradação de habitat nos campos, e que essas variações interagem com o habitat e afetam de forma diferencial os distintos componentes da diversidade. Por outro lado, a perda de habitat decorrente da silvicultura gera um impacto de maior magnitude, alterando a composição das comunidades de aves e favorecendo uma série de aves não campestres. Embora a degradação promovida pelo manejo do gado aumente a diversidade em nível de paisagem ao criar um mosaico de manchas de vegetação de alturas distintas, maior atenção deve ser dada à manutenção e recuperação de formações densas de herbáceas de grande porte, sob pena de futura perda de diversidade local e regional. Isso somente pode ser assegurado através de mudanças no regime do pastejo ou das técnicas de manejo da pastagem.

Entretanto, os aspectos abordados acima não exaurem o tema, mas servem de ponto de partida para futuras investigações. A mera presença de indivíduos de determinadas espécies em manchas de habitat pouco diz sobre aspectos de dinâmica de população. Como a qualidade dessas manchas afeta a natalidade e a mortalidade? As espécies negativamente afetadas pela perda e degradação de habitat campestre

conseguem manter populações viáveis nos remanescentes situados em depressões do terreno? A biota campestre teria condições de sobreviver em áreas de campo conservadas em meio aos talhões de eucalipto? Além dessas questões, também é fundamental investigar outros aspectos da diversidade, especialmente em termos funcionais. Que atributos são selecionados pelos impactos que geram perda e degradação de habitat? Quanto da diversidade funcional dos campos isso representa? Somente solucionando essas questões mais amplas é que poderemos de fato construir opções de manejo para a pecuária e silvicultura que possibilitem conciliar essas atividades econômicas com a conservação da biodiversidade nos campos temperados do sudeste da América do Sul.

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