Universidade Federal do Rio Grande do Sul
Instituto de Biociências
Programa de Pós-Graduação em Ecologia

ecologia
UFRGS

Tese de Doutorado

Padrões, processos e mecanismos de nucleação da vegetação lenhosa florestal nos campos do Planalto Nordeste do Rio Grande do Sul

Leandro da Silva Duarte

Porto Alegre, Agosto de 2007

Universidade Federal do Rio Grande do Sul

Instituto de Biociências

Programa de Pós-Graduação em Ecologia

Tese de Doutorado

Padrões, processos e mecanismos de nucleação da vegetação lenhosa florestal nos campos do Planalto Nordeste do Rio Grande do Sul

Leandro da Silva Duarte

Orientadores: Prof. Dr. Valério De Patta Pillar & Prof. Dra. Sandra Maria Hartz

Tese apresentada como pré-requisito para a obtenção do título de Doutor em Ciências – ênfase em Ecologia

Banca Examinadora:

Prof. Dr. Andreas Kindel (UFRGS)

Prof. Dr. João André Jarenkow (UFRGS)

Prof. Dr. Fábio Rubio Scarano (UFRJ)

Agradecimentos

Há muito a agradecer, e certamente não o bastante, a todas as pessoas que construíram comigo esta tese. Em primeiro lugar, agradeço a D. Antonia e Seu João Mar, meu pais, pelo suporte emocional e logístico. Agradeço profundamente a Esther, a quem dedico este trabalho, por acreditar sempre (muito mais do que eu próprio!). *Aní LeDodí VêDodí Li!*

Agradeço aos meus orientadores e amigos Valério D. Pillar e Sandra M. Hartz, pelos quatro anos de camaradagem e ensinamentos. Por extensão, agradeço aos membros dos Laboratórios de Ecologia de Populações e Comunidades e de Ecologia Quantitativa pela convivência fraterna e pelo suporte logístico.

Aos co-autores dos artigos, Melina M. G. dos Santos, Rafael E. Machado, Marcos B. Carlucci e Carla S. Fontana, meu muito obrigado pela ajuda inestimável! Em especial, agradeço a Rafael E. Machado pela concessão dos dados do seu Mestrado, fundamentais na maior parte da tese.

Agradeço aos professores e funcionários do Centro de Ecologia e PPG em Ecologia, em especial ao Prof. Dr. Andreas Kindel pelo apoio constante, e aos funcionários Marcelo Saraiva, Manoel Cunha e Silvana Barzotto. Agradeço também aos motoristas do IB-UFRGS, Armando, Luiz e Sandro, e ao Ailton, segurança, motorista e contador de causos.

Agradeço à direção do Instituto do Meio Ambiente da PUCRS, Dr. Jorge A. Villwock, Dra. Betina Blochtein e Dr. Ricardo S. P. Mello, à secretária Andréa S. S. Bueno, e aos funcionários do CPCN Pró-Mata Claiton, Rosângela, Rosane, Mineiro, Cleonir, Heronita, Cristiane, Leandro e Cleudi pela receptividade, por todo apoio logístico, e pela preocupação constante com o bom desenvolvimento de nossas atividades no Pró-Mata.

Muitas pessoas me ajudaram nas saídas de campo. Agradeço a todos e espero não esquecer nenhum nome: Cristian M. Joenck, Cristiano A. Isenhard, Esther R. S. Pinheiro, Fabiana Camargo, Fernanda T. Brum, Fernando S. Rocha, Gabriel S. Hofmann, Glauco Schussler, Juan Anza, Julia Hermann, Letícia P. Dadalt, Luciane Coletti, Luis Gustavo R. da Silva, Marcelo Saraiva, Marcos B. Carlucci, Melina M. G. dos Santos, Milena A. Fávero, Roberta Trois.

Agradeço ao CNPq pela bolsa de doutorado, e à CAPES e o Inter-American Institute for Global Change Research (IAI) pelo financiamento do projeto.

Obrigado a todos!

Sumário

Resumo

O modelo tradicional de dinâmica de expansão da floresta com *Araucaria* sobre os campos do Planalto Sul-brasileiro foi desenvolvido pelo naturalista Roberto Klein (1923-1992), e foi baseado no processo de nucleação florestal em áreas campestres. Estudos visando compreender o processo de estabelecimento de espécies de plantas lenhosas florestais em manchas de floresta com *Araucaria* isoladas em áreas campestres do Planalto Nordeste do Rio Grande do Sul foram desenvolvidos a partir da análise de padrões de colonização e mecanismos de dispersão de diásporos. Os estudos foram conduzidos no CPCN Pró-Mata PUCRS, em São Francisco de Paula, Estado do Rio Grande do Sul, Brasil. O CCapítulo 1 apresenta os principais eixos teóricos abordados ao longo da tese, seus referenciais históricos e contexto local. No CCapítulo 2 foi avaliado o papel de arbustos e árvores isoladas como sítios de colonização para espécies lenhosas florestais em áreas abertas. Foram encontradas mais plântulas de espécies florestais sob a copa de plantas-berçário (particularmente sob araucárias) do que em áreas abertas e as plântulas apresentaram diásporos dispersos principalmente por vertebrados, indicando a importância de árvores de *Araucaria angustifolia* como plantas-berçário no processo de colonização de sítios campestres por espécies florestais. Os capítulos 3, 4 e 5 discutem padrões de colonização de manchas florestais por espécies lenhosas florestais e mecanismos de dispersão de espécies florestais colonizadoras de manchas. Foram analisadas manchas florestais de tamanhos diferentes em área de campo nativo. No Capítulo 3 foram analisadas a composição de espécies (abundância relativa), a riqueza, a diversidade e os padrões de colonização em comunidades de plantas jovens nas manchas. Riqueza e diversidade foram positivamente correlacionadas com a

área da mancha; além disso, a ordenação das unidades amostrais de acordo com a abundância relativa de indivíduos jovens de espécies lenhosas indicou um gradiente nas comunidades de plantas jovens associado com a área da mancha. A razão entre a abundância de espécies residentes (presentes nas comunidades tanto como indivíduos jovens quanto como adultos) e colonizadoras (presentes nas comunidades somente como indivíduos jovens) aumentou de plantas-berçário para manchas grandes. Nestas últimas, o predomínio de espécies residentes nas comunidades de indivíduos jovens dificulta a imigração de novas espécies para as manchas, limitando a riqueza e a diversidade. No Capítulo 4 foram analisadas as estratégias de dispersão das espécies lenhosas colonizadoras das manchas. Foi avaliada a influência da filogenia e atributos de diásporos relacionados à atração de dispersores (DAT) sobre o *trade-off* tamanho de semente/número de sementes (SSNT) em espécies lenhosas colonizando manchas florestais, e em comunidades de plantas jovens presentes em manchas florestais de tamanhos diferentes. A alocação de energia para dispersão (número de sementes) em detrimento de sobrevivência da prole (tamanho das sementes) aumentou o sucesso no estabelecimento de espécies colonizadoras em manchas florestais somente quando as influências da filogenia e do DAT foram controladas através de análise de resíduos. A área da mancha exerceu uma pressão seletiva sobre o tamanho das sementes, especialmente quando as influências de filogenia e DAT foram removidas. No Capítulo 5 foi analisada a influência das interações entre plantas colonizadoras e frugívoros dispersores sobre a colonização de manchas florestais. A maioria das espécies lenhosas colonizando manchas de floresta com *Araucaria* apresentaram diásporos associados com dispersão por vertebrados. Interações entre plantas e frugívoros envolvendo aves de tamanho médio, a maioria frugívoras, associadas com habitats de borda e hábito migratório correlacionaram-se positivamente com manchas pequenas e grandes, enquanto aquelas

envolvendo aves residentes de tamanho grande, em sua maioria não-frugívoras e habitantes de áreas abertas e florestas associaram-se com plantas-berçário. Nossos resultados sugeriram um *trade-off* envolvendo a quantidade de reservas contidas na semente e a probabilidade do diásporo ser transportado por um frugívoro. No Capítulo 6, uma ampliação do modelo original de Klein é sugerida, e inclui outros níveis tróficos no processo de nucleação de manchas de floresta com *Araucaria* sobre os campos do Planalto Sul-brasileiro.

Palavras-chave: Nucleação, Dispersão de diásporos, Colonização por plantas, Manchas florestais, floresta com *Araucaria*, Campos de Cima da Serra

Abstract

The traditional model of expansion dynamics of the *Araucaria* forest over *Campos* grassland found in the southern Brazilian highlands was developed by the naturalist Roberto Klein (1923-1992), and was based on the forest nucleation process over grassland sites. Studies concerning the establishment of forest woody plant species into *Araucaria* forest patches isolated in grassland sites occurring in the Northeast Plateau of the Rio Grande do Sul were developed from analises of plant colonization patterns and diaspore dispersal mecanisms. Studies were conducted at the CPCN Pró-Mata PUCRS, São Francisco de Paula, Rio Grande do Sul State, Brazil. The Chapter 1 presents the main theoretical axes covered along the thesis, its historical backgrounds and its local context. In the Chapter 2 was evaluated the role of isolated shrubs and trees as colonization sites for forest woody species in open areas. We found more forest species seedlings beneath the nurse plant crowns (particularly beneath *Araucaria* trees) than in open areas, and the seedlings presented diaspores mainly dispersed by vertebrates, indicating the importance of *Araucaria angustifolia* trees as nurse plants in grassland colonization process by forest species. The chapters 3, 4 e 5 discuss patch colonization patterns and dispersal mecanisms of colonizer species in patches. Forest patches of different sizes and occurring in a native grassland were analyzed. In the Chapter 3 we analyzed the species composition (relative abundance), richness, diversity and colonization patterns in sapling communities in the patches. Richness and diversity were positively correlated with patch area; furthermore, the ordination of the sampling units according to the relative abundance of saplings from woody species has indicated gradient in the sapling communities associated with patch area. The ratio among the

abundance of resident species (those present in the communities both as saplings and adult individuals) and the abundance of colonizer species (those present in the communities only as saplings) increased from nurse plants to large patches. In the last, the prevailence of resident adults in the sapling communities made difficult the immigration of new species into the patches, limiting richness and diversity. In the Chapter 4, the dispersal strategies of woody species colonizing patches were analyzed. We evaluated the influence of phylogeny and diaspore attributes related to disperser attraction (DAT) on the seed size/number trade-off (SSNT) in woody species colonizing forest patches, and in sapling communities present in forest patches of different sizes. Energy allocation for dispersal (seed number) in detriment of offspring survival (seed size) increased the establishment success of the colonizer species in forest patches only when the influences of phylogeny and DAT were controlled through residual analysis. Patch area exerted a selective pressure on seed size, especially when the influences of phylogeny and DAT were removed. In the Chapter 5 we analyzed the influence of interactions between colonizer plants and disperser frugivores in the forest patch colonization. Most woody species colonizing *Araucaria* forest patches presented diaspore associated with vertebrate dispersal. Interactions between plants and frugivores involving medium-sized, mostly frugivorous birds, associated with edge habitats and migratory habit positively correlated with small and large patches, while those involving large-sized, resident, mostly non-frugivorous birds inhabiting open areas and forests were associated with nurse plants. Our results suggested a trade-off involving the seed reserve content and the probability of the diaspore being transported by a given frugivore. In the Chapter 6, an extension of the Klein´s original model is suggested, and includes other trophic levels in the process of *Araucaria* forest patch nucleation over the *Campos* grassland of the South Brazilian Plateau.

Keywords: Nucleation, Diaspore dispersal, Plant colonization, Forest patches, *Araucaria* forest, South Brazilian *Campos* grassland

Índice de Tabelas

Capítulo 2.

Capítulo 3.

Capítulo 4.

Capítulo 5.

Índice de Figuras e Pranchas

Capítulo 1.

Capítulo 2.

Capítulo 3.

Capítulo 4.

Capítulo 5.

Capítulo 6.

Capítulo 1. Introdução

Apresentação

No Planalto nordeste do Estado do Rio Grande do Sul encontra-se uma das mais belas paisagens do Sul do Brasil, conhecida popularmente como Campos de Cima da Serra. Esta região caracteriza-se pela ocorrência de extensas áreas de campo entremeadas por manchas de floresta com *Araucaria* de tamanhos variados, constituindo um mosaico vegetacional (Klein 1960, Rambo 1994, Fig. 1).

Fig. 1. *Mosaico de campo e de floresta com* Araucaria *em São Francisco de Paula, Rio Grande do Sul (Brasil). Notar as pequenas manchas florestais e as araucárias isoladas (seta) em meio ao campo. Foto: L. S. Duarte (2003).*

As florestas com *Araucaria* caracterizam-se pela ocorrência expressiva de espécies de origem austral-antártica (temperadas) (Rambo 1951). Além da *Araucaria angustifolia*, destacam-se neste contingente temperado espécies arbóreas tais como *Podocarpus lambertii* (Podocarpaceae), *Drimys* sp. (Winteraceae), *Scutia buxifolia* (Rhamnaceae), entre outras, além de espécies arbustivas, *e.g.* *Berberis laurina* (Berberidaceae), lianas, como *Fuchsia regia* (Onagraceae) e herbáceas, *e.g.* *Acaena eupatoria* (Rosaceae). Apesar desta particularidade, a composição florística predominante nos pinhais consiste de espécies de origem tropical (Rambo 1951, Rambo 1956). As matas com *Araucaria angustifolia* estendem-se no Brasil pelos Estados de Santa Catarina, Paraná e São Paulo. No Rio de Janeiro e em Minas Gerais, as araucárias surgem em pequenos agrupamentos ou isoladas, em altitudes superiores a 1000 metros. O limite altitudinal inferior dos pinhais localiza-se entre 300 e 600 metros nos Estados do sul do Brasil e aumenta rumo ao norte, atingindo 2000 metros em Itatiaia, no Rio de Janeiro (Franco et al. 2005). Na Argentina, florestas com *A. angustifolia* ocorrem na Província de Misiones (Hueck 1972), enquanto Reitz et al. (1978) e Backes (1999) registraram a ocorrência de pinhais no Paraguai.

Desde o início do século 20, a dinâmica entre a floresta com *Araucaria* e os campos do Planalto vem sendo alvo de discussão entre naturalistas. Nos primeiros anos do século XX, Lindman já considerava os campos uma formação mais antiga do que as florestas com araucária (Lindman 1906). Na década de 1950, o padre Balduíno Rambo, na sua “Fisionomia do Rio Grande do Sul” (Rambo 1994), também admitiu esta hipótese como a mais adequada para explicar a dinâmica ecológica entre os campos e as florestas dos Campos de Cima da Serra. Segundo ele, os campos do Planalto estariam sendo progressivamente substituídos pelas florestas. “A vegetação do Rio Grande do Sul tende para o mato”, escreveu o naturalista. Recentemente, esta hipótese vem sendo confirmada através de estudos palinológicos (Behling 2002, Behling &

Pillar 2007) e ecológicos (Oliveira & Pillar 2004). Porém, atividades humanas comuns na região, como as queimadas, a criação de gado bovino e a atividade madeireira tendem a retardar o avanço das florestas sobre os campos, por dificultarem o estabelecimento de espécies vegetais florestais em áreas abertas (Heringer & Jacques 2001). Assim, a paisagem que se observa nesta região é resultante de duas forças opostas. De um lado, a dinâmica natural do ecossistema campo-floresta, determinado por múltiplas interações entre clima, solo e organismos, tende a favorecer o avanço da Floresta com *Araucaria* sobre o campo. De outro, as atividades humanas predominantes na região retardam o avanço florestal, garantindo a permanência do mosaico vegetacional.

Durante meu doutorado, desenvolvi estudos visando compreender aspectos relativos à dinâmica de expansão da floresta com *Araucaria* sobre os campos do Planalto nordeste do Rio Grande do Sul. O foco principal destes estudos foi o processo de estabelecimento de espécies de plantas lenhosas florestais no campo e em manchas florestais isoladas em áreas campestres. A partir da análise de padrões de colonização de manchas florestais por espécies lenhosas, foi possível analisar mecanismos de dispersão da vegetação lenhosa relacionados à colonização de manchas de floresta com *Araucaria*.

A dinâmica do mosaico campo-floresta com *Araucaria*, segundo Roberto M. Klein (1923-1992)

Na década de 1960, o naturalista Roberto M. Klein propôs um modelo de dinâmica das comunidades florestais e campestres do Planalto Sul-brasileiro (Klein 1960), segundo o qual a expansão dos pinhais sobre os campos ocorreria a partir: 1) do avanço gradual da vegetação da borda florestal sobre o campo adjacente, demonstrado recentemente através da análise de imagens por técnicas de geoprocessamento (Oliveira & Pillar 2004), e 2) do estabelecimento de espécies arbóreas pioneiras sobre áreas de campo, iniciando aí o processo de nucleação de manchas florestais. O termo *nucleação* foi definido por Yarranton & Morrison (1974) como sendo o processo de estabelecimento e desenvolvimento de um determinado tipo de comunidade em meio a outro, através do estabelecimento de um ou poucos indivíduos-núcleo de espécies pioneiras da comunidade em expansão de forma isolada em meio à comunidade predominante. Segundo o modelo de Klein, os campos do Planalto seriam sucessivamente invadidos por um determinado número de espécies de arbustos e pequenas árvores que atuariam como estágios pioneiros da vegetação (os núcleos). Estes indivíduos possibilitariam o estabelecimento de outras espécies arbóreas por tornarem o ambiente ao seu redor mais propício ao desenvolvimento das plantas, dando origem à formação florestal. O modelo de Klein (1960) apresenta duas características teóricas fundamentais:

1) *É um modelo unitrófico*: mudanças estruturais na vegetação são causadas por variações climáticas e edáficas, e determinam a variação nos padrões observados em outros níveis tróficos.

2) *É um modelo de nicho*: à medida que espécies tolerantes a áreas abertas estabelecem-se no campo, alteram o ambiente, possibilitando o estabelecimento de outras espécies com exigências ambientais distintas, ou mais especificamente, tolerantes à sombra. Neste modelo, o processo de transporte de diásporos não afeta o processo de desenvolvimento das comunidades das manchas. O estabelecimento diferencial de algumas espécies é unicamente uma função de sua tolerância ao novo ambiente.

Testando o modelo de Klein

O modelo de nucleação de Klein representou o ponto de partida a partir do qual podemos dar um passo adiante na investigação dos mecanismos subjacentes à dinâmica de nucleação dos pinhais. Como foi dito anteriormente, atividades humanas como queimadas e criação de gado bovino dificultam o avanço da vegetação florestal sobre o campo. Portanto, para analisar empiricamente o modelo de nucleação de Klein (1960), foi necessário encontrar uma área onde tais atividades não ocorressem ou, ao menos, tivessem sido interrompidas há um tempo suficiente para permitir o processo de estabelecimento da vegetação florestal no campo.

O Centro de Pesquisas e Conservação da Natureza Pró-Mata (CPCN Pró-Mata), localizado no Município de São Francisco de Paula a aproximadamente 900 metros de altitude, sob as coordenadas 29°28’S e 50°13’W, tem 4500 hectares de área total (Fig. 2).

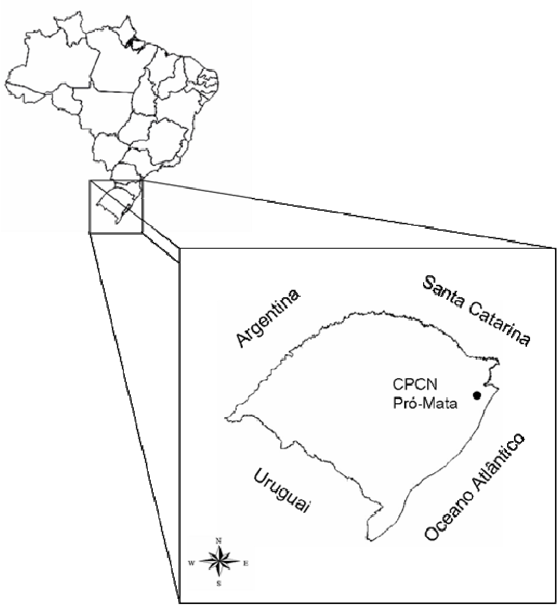

Fig. 2. *Localização do Centro de Pesquisas e Conservação da Natureza Pró-Mata - PUCRS, São Francisco de Paula, Rio Grande do Sul (Brasil).*

A vegetação do Pró-Mata é constituída por áreas de campo, onde se encontram manchas (regionalmente denominadas *capões*) de floresta com *Araucaria*, e por formações de Mata Atlântica. Desde 1993, queimadas e criação de gado foram interrompidas na área, permitindo a regeneração da floresta nos capões. Além disso, vem-se observando um acúmulo de biomassa vegetal, bem como o intenso estabelecimento de vegetação lenhosa na formação campestre (Oliveira & Pillar 2004). A área estudada constituiu-se numa mancha de campo de aproximadamente 78 hectares, circundada por floresta contínua, e na qual se observam diversos capões florestais de tamanhos variados (Machado 2004), como pode ser observado na figura 3.

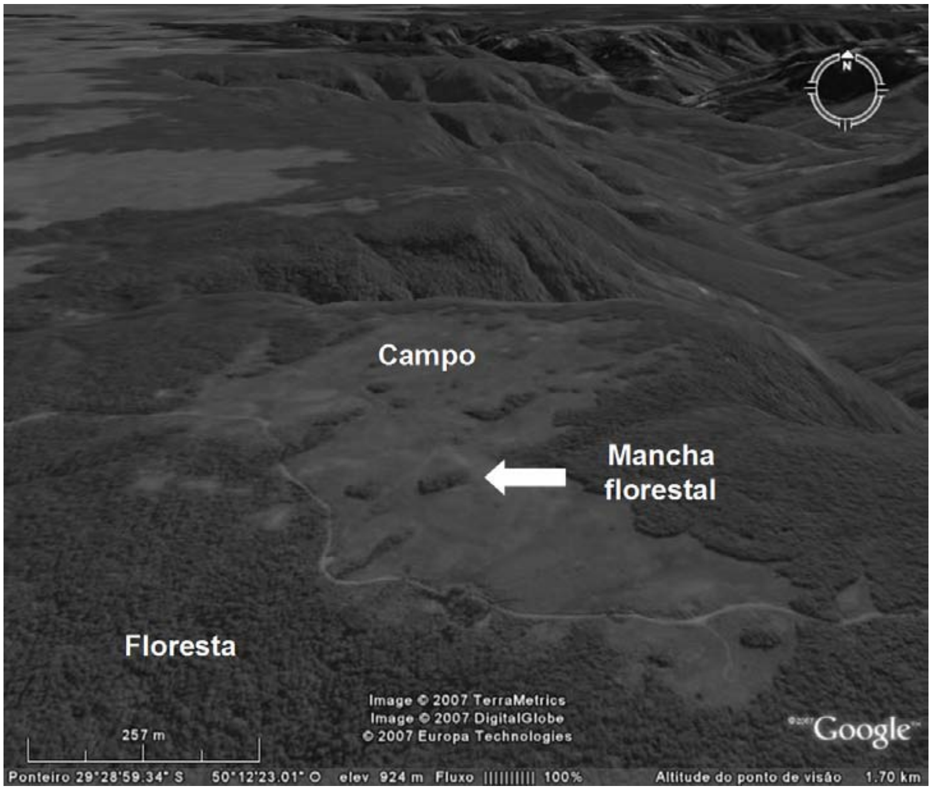

Fig. 3. *Vista em perspectiva da área de estudo no CPCN Pró-Mata PUCRS. Fonte: Google Earth (2007), disponível em http://earth.google.com.*

As plantas-berçário como núcleos de colonização florestal em áreas campestres

De acordo com o modelo de Klein (1960), arbustos e árvores isoladas em meio ao campo serviriam como núcleos de estabelecimento de espécies florestais, ou “plantas-berçário” segundo alguns autores (Franco & Nobel 1989, Tewksbury & Lloyd 2001, Scarano 2002). Eu considerei este um bom ponto de partida para avaliar empiricamente o modelo de nucleação. Basicamente, busquei responder três questões: 1) O estabelecimento de espécies lenhosas oriundas da floresta com *Araucaria* é maior sob a copa de arbustos e árvores isolados no campo em relação a áreas abertas adjacentes aos mesmos?; 2) O estabelecimento de espécies lenhosas oriundas da floresta com *Araucaria* ocorre preferencialmente sob a copa de determinadas espécies de plantas-berçário em relação às outras?; 3) Quais os mecanismos que fazem da araucária uma planta-berçário eficiente? Estas três questões são abordadas Capítulo 2 da tese.

Detectando padrões de colonização em manchas florestais

Os diferentes tipos de manchas de floresta com *Araucaria* espalhados nos campos do Planalto nordeste do Rio Grande do Sul poderiam representar diferentes estágios sucessionais do avanço da floresta sobre o campo? Segundo o modelo de Klein (1960), a resposta seria sim. Porém, o processo de nucleação florestal é um fenômeno bastante complexo. Capões pequenos podem ser muito mais antigos do que capões mais extensos. Assim, a única forma de avaliar direta e cronologicamente o desenvolvimento dos capões seria através do monitoramento periódico de áreas amostrais permanentes. Para tanto, seria necessário executar projetos de longo prazo, talvez na escala de décadas, para que resultados satisfatórios fossem obtidos.

Considerando estas dificuldades, propus uma abordagem de estudo que pudesse ser executada em curto período de tempo, e que permitisse avaliar, mesmo que de forma indireta, o processo de nucleação dos capões de floresta com *Araucaria*. Parti do pressuposto fundamental de que variações estruturais nos capões podem ser usadas em substituição ao tempo de formação (idade) dos mesmos. Para tanto, baseei-me no argumento de Pickett (1989), que salientou a importância do ambiente operacional, isto é, do conjunto de condições e interações que controlam o comportamento de um ecossistema, para a construção de modelos de dinâmica das comunidades. Segundo o autor, atributos estruturais, tais como padrões de colonização, regime de distúrbio e migração de espécies, auxiliam na busca pelo entendimento de processos ecológicos de escala temporal mais ampla. Como o processo de nucleação envolve a expansão radial do núcleo florestal, considerei a área da mancha uma variável adequada para caracterizar o gradiente estrutural nos capões de floresta com *Araucaria*. Todas as manchas selecionadas localizaram-se no CPCN Pró-Mata, na mesma área de campo descrita para o capítulo anterior. Este fato propiciou uma condição de estudo muito especial, visto que o tempo desde a supressão dos distúrbios gerados pelas queimadas e pastejo, que dificultam o estabelecimento das plantas no campo e nos capões, foi o mesmo para toda a área (≅ 10 anos). Ou seja, a retomada do processo de nucleação pós-distúrbio foi possibilitada ao mesmo tempo em todas as manchas, permitindo associar eventuais padrões de variação no processo de nucleação ao gradiente estrutural das manchas.

Tomando essas condições e pressupostos em consideração, avaliei como a estrutura (riqueza, diversidade e abundância relativa de espécies) de comunidades de plantas lenhosas jovens estabelecidas em manchas de floresta com *Araucaria* variou em relação ao gradiente de tamanho das manchas. Além disso, as assembléias de plantas jovens foram analisadas funcionalmente em relação à origem dos indivíduos presentes nas comunidades; espécies presentes apenas como indivíduos jovens foram classificadas como colonizadoras, enquanto aquelas presentes tanto como indivíduos jovens quanto como adultos foram consideradas residentes. Utilizando estas variáveis-resposta, a influência do gradiente estrutural das manchas neste padrão foi avaliada. Estas questões são abordadas no Capítulo 3 da tese.

De padrões a mecanismos

O conjunto de espécies colonizadoras presentes nas manchas florestais (ver Capítulo 3) representa um subconjunto de espécies ocorrentes na matriz florestal, que se dispersa desta última para as manchas. Se eventuais variações no padrão de colonização das manchas decorrem unicamente da tolerância das espécies colonizadoras às características ambientais presentes nas manchas, como prediz o modelo de Klein (1960), então os padrões de dispersão de diásporos destas espécies em comunidades de plantas jovens nas manchas não devem apresentar variações associadas à gradientes estruturais das manchas. Caso contrário, um novo fator (estratégias de dispersão) deve ser incorporado ao modelo original.

Características funcionais dos diásporos, isto é, das unidades de dispersão (Van der Pijl 1982) das espécies colonizadoras, tais como tipo, tamanho, cor, além de tamanho das sementes e número de sementes por diásporo, fornecem informações valiosas sobre estratégias de dispersão destas espécies. Desta forma, a partir de *padrões* de colonização encontrados nas manchas florestais, podemos analisar *mecanismos* de dispersão envolvidos no processo. Contudo, apesar desta abordagem metodológica (mecanismos a partir de padrões) oferecer muitas possibilidades de estudo, ela implica obrigatoriamente em que o fator filogenético subjacente aos atributos avaliados seja considerado (ver Westoby et al. 1995). As características dos diásporos de uma determinada espécie de planta podem não representar tendências adaptativas atuais, pois o surgimento de atributos não necessariamente ocorre de forma independente em espécies pertencentes a um dado clado. Por exemplo, se um atributo *i* é característico do gênero G, e as espécies A e B pertencem a G, então A e B apresentarão *i*. Se A e B co-ocorrerem num dado tipo de mancha florestal, o atributo *i* poderá tanto representar um atributo ecológico relevante no processo de colonização da mancha, quanto ser meramente um reflexo da proximidade filogenética entre A e B.

Mecanismos de dispersão associados à colonização de manchas florestais foram avaliados sob dois enfoques distintos. Primeiramente, foram analisados atributos das sementes (tamanho, número) das plantas colonizadoras, os quais podem indicar *trade-offs* relacionados a investimento em dispersão (muitas sementes por diásporo) vs. sobrevivência da prole (sementes grandes) (e.g. Leishman et al. 2000). As estratégias de dispersão das espécies colonizadoras de manchas florestais são abordadas no Capítulo 4 da tese.

Finalmente, informações sobre os agentes dispersores dos diásporos das plantas (vento, animais), indicam como as espécies colonizadoras interagem com outros compartimentos ecológicos no processo de colonização das manchas florestais (e.g. Ridley 1930, van der Pijl 1982). No caso das plantas dispersas pela fauna, ainda é possível analisar atributos relacionados à atração de dispersores, como tipo, tamanho e cor dos diásporos (van der Pijl 1982), constrastando-os com informações a respeito de interações com frugívoros ocorrentes na área de estudo. A associação entre os atributos de diásporos das espécies colonizadoras e seus respectivos agentes dispersores foi analisada no Capítulo 5 da tese. Finalmente, o Capítulo 6 fornece uma síntese conclusiva abrangendo os diferentes capítulos da tese. Ressalto que o Capítulo 2 da tese encontra-se formatado de acordo com as normas do periódico *Austral Ecology*. Os Capítulos 3, 4 e 5 estão formatados de acordo com as normas do periódico *Journal of Vegetation Science*.

Referências

Backes, A. 1999. Condicionamento climático e distribuição geográfica de *Araucaria angustifolia* (Bertol.) Kuntze no Brasil – II. *Pesquisas (Botânica)* 49: 31-52.

Behling, H. 2002. South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeo. Palaeoclim. Palaeoecol.* 177: 19-27.

Behling, H. & Pillar, V.D. 2007. Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. *Phil. Trans. Royal Soc. London Biol. Sci.* 362: 243-251.

Franco, A.C., Duarte, H.M., A. Geßler, A., Mattos, E.A., Nahm, M., Rennenberg, H., Ribeiro, K.T., Scarano, F.R., Lüttge, U. 2005. In situ measurements of carbon and nitrogen distribution and composition, photochemical efficiency and stable isotope ratios in *Araucaria angustifolia*. *Trees* 19: 422-430.

Franco, A.C. & Nobel, P.S. 1989. Effect of nurse plants on the microhabitat anf growth of cacti. *J. Ecol.* 77: 870-886.

Heringer, I. & Jacques, A.V.A. 2001. Adaptação das plantas ao fogo: enfoque na transição campo-floresta. *Ciência Rural 31*: 1085-1090.

Hueck, K. 1972. *As Florestas da América do Sul*. Ed. UnB- Ed. Polígono, São Paulo, Brasil.

Klein, R.M. 1960. O aspecto dinâmico do pinheiro brasileiro. *Sellowia* 12: 17-51.

Leishman, M., Wright, I.J., Moles, A.T. & Westoby, M. 2000. The evolutionary ecology of seed size. In: Fenner, M. (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*, 2a ed. p. 31-57. CAB International, Wallingford, Reino Unido.

Lindman, C.A.M. 1906. *A vegetação no Rio Grande do Sul*. Livraria Universal de Echenique Irmãos, Porto Alegre, Brasil.

Machado, R.E. 2004. *Padrões Vegetacionais em Capões de Floresta com Araucaria no Planalto Nordeste do Rio Grande do Sul, Brasil*. Dissertação de Mestrado, UFRGS, Porto Alegre, Brasil.

Oliveira, J.M. & Pillar V.D. 2004. Vegetation dynamics on mosaics of *Campos* and Araucaria forest between 1974 and 1999 in Southern Brazil. *Comm. Ecol.* 5: 197-202.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (ed.) *Long-Term Studies in Ecology – Approaches and Alternatives*. p. 110-135. Springer-Verlag, Nova Iorque, EUA. 214 p.

Rambo, B. 1951. O elemento andino no pinhal riograndense. *Anais Bot. HBR* 3: 7-39.

Rambo, B. 1956. A flora fanerogâmica dos Aparados riograndenses. *Sellowia* 7: 235-298.

Rambo, B. 1994. *A Fisionomia do Rio Grande do Sul*. 3a ed., Ed. Unisinos, São Leopoldo, Brasil.

Reitz, R., Klein, R.M. & Reis, A. 1978. *Projeto Madeira de Santa Catarina*. Herbário Barbosa Rodrigues, Itajaí, Brasil.

Ridley, H.N. 1930. *The Dispersal of Plants Throughout the World.* L Reeve and Co, Kent, Reino Unido.

Scarano, F.R. 2002. Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic Rainforest. *Ann. Bot.* 90: 517-524.

Tewksbury, J.J. & Lloyd, J.D. 2001. Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* 127: 425-434.

Van der Pijl, L. 1982. *Principles of Dispersal in Higher Plants.* Springer-Verlag, Berlim, Alemanha.

Westoby, M, Leishman, M.R. & Lord, J.M. 1995. On misinterpreting the 'phylogenetic correction'. *J. Ecol.* 83: 53-534.

Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *J. Ecol.* 62: 417-428.

Capítulo 2. Role of nurse plants in *Araucaria* Forest expansion over grassland in south Brazil[1]

LEANDRO DA S. DUARTE*, MELINA M.G. DOS-SANTOS, SANDRA M. HARTZ AND VALÉRIO DE PATTA PILLAR.

Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, A. Bento Gonçalves 9500 CP 15007, Porto Alegre, RS 91501-970, Brazil (E-mail: lsduarte@ecologia.ufrgs.br)

*Corresponding author

Resumo

A expansão da floresta com *Araucaria* sobre o campo ocorre sob condições de clima úmido e baixo índice de distúrbio e é hipotetizado que árvores isoladas estabelecidas no campo facilitam o estabelecimento de espécies lenhosas florestais sob suas copas. A floresta com *Araucaria angustifolia* é um tipo particular de floresta Atlântica brasileira e constitui o principal tipo florestal do Planalto Sul-brasileiro, geralmente formando mosaicos com campos naturais. Os objetivos deste artigo foram avaliar o papel de arbustos e árvores isoladas como sítios de colonização para plântulas de espécies lenhosas da floresta com *Araucaria* sobre o campo, determinar quais espécies funcionam como plantas-berçário preferenciais no processo e a importância da dispersão de diásporos por vertebrados na estrutura de comunidades de plântulas sob plantas-berçário. O estudo foi conduzido em São Francisco de Paula, Estado do Rio Grande

---

[1] Artigo publicado no periódico *Austral Ecology* (2006) 31:520-528 (doi:10.1111/j.1442-9993.2006.01602.x)

do Sul, onde nós amostramos arbustos e árvores isoladas em campo natural próximo a bordas com floresta com *Araucaria*. Plântulas foram contadas e identificadas, e síndromes de dispersão das plântulas, bem como seu tamanho e cor, foram registradas. Nós detectamos onze espécies lenhosas com potencial papel nucleador na colonização do campo por espécies florestais. Foram encontradas mais plântulas de espécies florestais sob a copa de plantas-berçário do que em áreas abertas e as plântulas apresentaram diásporos dispersos principalmente por vertebrados. Além disso, mais plântulas foram encontradas sob a copa de *Araucaria angustifolia* do que sob a copa de outras espécies de plantas-berçário. Nós concluímos que árvores de *A. angustifolia* estabelecidas no campo agem como plantas-berçário, atraindo aves dispersoras que promovem a colonização do sítio por outras plântulas de espécies florestais, e que sob baixos níveis de distúrbio no campo, a conservação de assembléias de vertebrados frugívoros pode aumentar a expansão florestal sobre o campo nativo e também facilitar a regeneração de áreas florestais degradadas.

Palavras-chave: Floresta com *Araucaria*, campos, dinâmica de comunidades, facilitação, plantas-berçário, dispersão de sementes por vertebrados

Abstract

Araucaria Forest expansion over grassland takes place under wet climate conditions and low disturbance and it is hypothesized that isolated trees established on grassland facilitate the establishment of forest woody species beneath their canopies. Forest with *Araucaria angustifolia* is a particular type of Brazilian Atlantic Forest and the main forest type on the highland plateau in South Brazil, often forming mosaics with natural *Campos* grassland. The objectives of this paper were to evaluate the role of isolated shrubs and trees as colonisation sites for seedlings of Araucaria Forest woody species on grassland, to determine which species function as preferential nurse plants in the process and the importance of vertebrate diaspore dispersal on the structure of seedling communities beneath nurse plants. The study was conducted in São Francisco de Paula, Rio Grande do Sul State, where we sampled isolated shrubs and trees in natural grassland near Araucaria Forest edges. Seedlings were counted and identified, and seedling diaspore dispersal syndromes, size and colour were registered. We detected eleven woody species with a potential role in nucleating grassland colonisation by forest species. Beneath the canopies of nurse plants more forest species seedlings were found compared to open field grassland and the seedlings had diaspores mostly dispersed by vertebrates. Also, more seedlings were found under the canopy of *Araucaria angustifolia* than beneath other nurse plant species. We conclude that *A. angustifolia* trees established on grassland act as nurse plants, by attracting disperser birds that promote colonisation of the site by other forest species seedlings, and that under low level of grassland disturbance, conservation of frugivorous vertebrate assemblages may increase forest expansion over natural grassland and also facilitate the regeneration of degraded forest areas.

Key words: Araucaria Forest, *Campos* grassland, community dynamics, facilitation, nurse plants, vertebrate seed dispersal

Introduction

Forest expansion over grassland may occur under certain environmental conditions, such as wet climate and low level of disturbance, but the relevant mechanisms involved in this spatial ecological process are not well understood (Archer *et al.* 1988; Pillar 2003). Forest species colonising open grassland should be able to tolerate environmental conditions extremely different from those commonly found in forests, such as high variation in temperature and soil moisture levels, high transpiration rates and grass competition (Scholes & Archer 1997; Sankaran *et al.* 2004). Isolated trees and shrubs established on grassland can facilitate (*sensu* Bruno *et al.* 2003) the germination and growth of forest woody species beneath their canopies. This process has been called the nurse plant effect (Franco & Nobel 1989; Tewksbury & Lloyd 2001; Scarano 2002). Many authors have pointed out the importance of nurse plants in tree species colonisation of open habitats (Guevara *et al.* 1992; Callaway 1995; Slocum & Horwitz 2000; Slocum 2001; Holl 2002; Scarano 2002). However, most studies deal with forest recovery over degraded areas. Forest expansion over naturally occurring grassland ecosystems has received less attention from ecologists.

Scarano (2002) reviewed the role of nurse plants in facilitating plant establishment in ecosystems under extreme environmental condition, such as open *restingas* and high altitude rock outcrops. The author suggested that nurse plant species have stress tolerance traits enabling their establishment in extreme conditions. Furthermore, the presence of nurse plants ameliorate environmental conditions for less stress tolerant species, promoting community development. We consider grassland-forest transitions as such a stressful situation. Thus, we could hypothesize that nurse plants species function in a similar manner in both Scarano’s extreme condition ecosystems and grassland-to-forest transition dynamics, facilitating forest species establishment on grassland

and promoting forest expansion. Callaway (1995) suggests that the effectiveness as a nucleus plant may vary among plant species, and that facilitation is promoted mainly by alteration of resource availability and environmental conditions by nurse plants, such as light, temperature, soil moisture and nutrients. Other authors have stressed the major role played by nurse plants as perches used by seed dispersal birds (Uhl 1987; Guevara *et al.* 1992; McClanahan & Wolfe 1993; Toh *et al.* 1999; Galindo-González *et al.* 2000; Slocum & Horwitz 2000; Zimmerman *et al.* 2000; Aukema and Martinez-del Rio 2002; Holl 2002; Shiels &Walker 2003). Several authors emphasize the important role of shrubs and trees established on grassland in attracting frugivorous birds (Wunderle Jr. 1997; Toh *et al.* 1999; Shiels & Walker 2003). Pioneer woody species are used as perches by these birds, increasing seed rain under the nurse plant crown area and promoting forest species seedling establishment.

Forests with *Araucaria angustifolia* (Araucariaceae) constitute the main forest type on the highland plateau in South Brazil at altitudes above 500 m a.s.l. (Duarte & Dillenburg 2000). Araucaria Forest communities are characterised by the presence of woody species phytogeographically related to Austral-Antartic and Andean floras (Rambo 1951; Waechter 2002). The most physiognomically important tree species is *Araucaria angustifolia*. Some other typical species found in these forests are *Podocarpus lambertii*, *Drimys brasiliensis*, *Dicksonia sellowiana*, and several species of Myrtaceae, Melastomataceae and Lauraceae. Oliveira-Filho and Fontes (2000) recognized Brazilian Araucaria Forest as a particular type of Atlantic Forest.

Araucaria forests in South Brazil often form mosaics with *Campos* grassland, as gallery forests along streams and as forest islands on the higher portions of the undulated relief (Rambo 1994; Duarte *et al.* 2002). According to Behling *et al.* (2004), a change from a drier to a moister climate, that occurred *ca.* 3000 years before the present, favoured Araucaria Forest expansion, especially in the last millennium. Nowadays, these forests can naturally expand over grassland (Rambo 1956; Klein 1960; Hueck 1972; Oliveira & Pillar 2004). However, burning and domestic cattle grazing have likely slowed natural forest expansion over *Campos* grasslands (Pillar 2003). Klein (1960) proposed that Araucaria Forest expansion starts when pioneer shrubs and tree species invade grasslands and promote the establishment of other forest woody species below their canopies, starting a forest patch. In regions with high rainfall levels a major proportion of plant species have diaspores (fruits and/or seeds) dispersed by animals (Howe & Smallwood 1982; Tabarelli & Peres 2002). Kindel (2002) found that about 90% of the tree species in two Araucaria Forest sites in Northeast Rio Grande do Sul had animal dispersed diaspores. However, the impact of vertebrate seed dispersal on the dynamics of araucaria forests remains poorly understood.

In this paper we report evidence to evaluate (1) the role of isolated shrubs and trees as potential nurse plants for Araucaria Forest woody species colonisation in *Campos* grassland; (2) which species function as preferential nurse plants and (3) the importance of vertebrate diaspore dispersal on the structure of seedling communities occurring beneath nurse plant canopies.

Methods

Study site

The study was conducted at 29°28'S and 50°13'W, in the Pró-Mata Research and Nature Conservation Centre (CPCN Pró-Mata). The Centre has 4500 ha and is located in São Francisco de Paula, Rio Grande do Sul State, southern Brazil. The regional climate is classified according to the Köppen system as Cfb (Dalmagro & Vieira 2005). The regional annual mean temperature is *ca.* 14.5°C, with negative temperatures occurring from April to November (Backes 1999), and high rainfall levels occurring throughout the year, and an annual mean rainfall of 2252 mm (Backes *et al.* 2000).

The study site consisted of *ca.* 78 ha *Campos* grassland surrounded by Araucaria Forest, situated on a plateau at *ca.* 900 m a.s.l. In the grassland, small forest nuclei, regionally called *capões* are found, in different degrees of development (Machado 2004). Cattle grazing and burning practices were terminated in 1993, allowing increasing regeneration of the forest and more biomass accumulation and woody plant establishment in the grassland (Oliveira & Pillar 2004). These conditions generated a tall and dense grassland matrix composed of caespitose grasses (*Andropogon lateralis,* up to 0.8 m high) and shrubs (*Baccharis uncinella*, *Calea phyllolepis*), which tend to suppress short grasses and other herbaceous species (Oliveira & Pillar 2004).

Sampling methods

Isolated trees and shrubs (hereafter called nurse plants) were randomly sampled in the study site in April 2003. We considered a tree to be isolated if it had no neighbour woody plant touching its crown. Starting from an arbitrarily defined initial point, we walked a 50 m straight path following a pre-determined direction (N, S, E or W). At the end of the path, the nearest isolated woody plant that was at least 1.5 m high was tagged and identified. Then, a new direction was chosen and the process repeated 100 times. The total area inside the perimeter connecting the outermost nurse plants sampled was approximately 16.4 ha. Each sampled individual was described by architectural (life form– shrub or tree, height, crown area) and ecological traits (forest occurrence and diaspore dispersal type – by vertebrates or other).

After nurse plant sampling, we quantified the abundance of seedlings beneath nurse plants. We sampled seedlings from October to December 2003. We compared the occurrence of seedlings beneath nurse plants with that in the open field. For this, after choosing a direction from the nurse plant (N, S, E or W), we sampled a square area outside its crown area, with the sides equal to the corresponding nurse plant crown diameter. Each open field quadrat was located away from the respective nurse plant by a distance equal to the crown diameter of the latter. Seedlings of forest woody species were counted and identified, and seed dispersal syndromes, diaspore size and colour were recorded, based mainly on the literature or by consulting experts. We classified diaspores into two categories (small or large) following Janson (1983). Seedling populations were separated into two height classes (0-50 cm and >50 cm), in order to prevent a bias related to the effect of nurse plant age on the abundance of seedlings.

Data analysis

We used ordination analysis to evaluate the association between isolated woody plant species and architectural/ecological traits. The ordination method used was a principal coordinates analysis (PCoA), computed on Euclidean distances between sampling units (plant species). Architectural/ecological traits correlated with the two first ordination axes ($r \geq 0.6$) were used to produce a biplot with sampling units. The stability of ordination axes was evaluated by bootstrapped auto-resampling (Pillar 1999). We used analysis of variance with randomisation testing (Manly 1997) to compare (1) the total number of seedlings beneath the crown area of nurse plants with that in the open field, and (2) the density of seedlings beneath different groups of nurse plant species. The test criterion was the sum of square Euclidean distances between groups of sampling units (Q_b statistic, Pillar & Orlóci 1996). In order to evaluate the association between nurse plant and seedling species, we used PCoA, computed on Euclidean distances between variables (relative frequencies of the seedling species).

Ordination of isolated woody plants was performed using the software SYNCSA (Pillar 2002). All other analyses were performed using the software MULTIV v. 2.3.10 (Pillar 2004).

Results

We found eleven woody species occurring isolated on *Campos* grassland (Table 1). The wind-dispersed *Baccharis uncinella* was the most abundant species, with 63% of sampled individuals. The second more abundant species (12%) was *Pinus elliotti*, a wind-dispersed alien tree species cultivated in neighbouring properties. Wind-dispersed individuals comprised 83% of total abundance. The most abundant vertebrate-dispersed woody species were *Myrceugenia euosma* and *Araucaria angustifolia*, representing 8% and 6% of total abundance, respectively. An ordination diagram indicated the clumping of isolated woody plants into four distinct groups, strongly associated with dispersal syndrome (vertebrate *vs.* other types), life form (trees *vs.* shrubs), plant height and forest occurrence (Fig. 1).

Our survey found a significantly higher number of seedlings of forest woody species beneath the nurse plants in comparison to open field grassland (Fig. 2). However, the occurrence of seedlings differed among nurse plant groups (Fig. 3). Five woody species had seedlings ≤ 50 cm tall below their crowns, namely, *Araucaria angustifolia, Agarista nummularia*, *Agarista eucalyptoides*, *Baccharis uncinella* and *Pinus elliotti.* Seedlings taller than 50 cm were found beneath *A. angustifolia*, *B. uncinella*, *Myrceugenia euosma* and *P. elliotti*. Despite their broad occurrence in the study area (see Table 1), *B. uncinella* and *P. elliotti* had very low densities of seedlings beneath their crowns. We found a much higher seedling density beneath araucaria individuals than under other nurse plant species, for both seedling height classes (Fig. 3A and B). Indeed, 79% (for seedlings ≤ 50 cm tall) and 91% (for seedlings taller than 50 cm) of the total sum of squares between groups for density of seedlings were due to a unique orthogonal contrast, comparing *A. angustifolia* nurse plants to all the other nurse plant species. The “Others” group, formed by six species (Table 1), also showed a high seedling density in both height classes. This group also contained species potentially important as establishment foci for forest woody species, like *Agarista eucalyptoides* and *Myrsine lorentziana*, but the low occurrence of those species in our samples made it difficult to come to a more accurate conclusion.

We found nine forest woody species as seedlings ≤50 cm tall beneath nurse plants. Seedlings taller than 50 cm were represented by six species (Table 2). *Myrsine lorentziana* was the most abundant seedling species found under nurse plant crowns (Table 2). Among the shorter seedlings, *Miconia hyemalis* was the second most abundant species; Myrtaceae was the third and *Araucaria angustifolia* the fourth. For seedlings taller than 50 cm, *Siphoneugena reitzii* was the second most abundant species. Other species represented 2% or less of total abundance. Ordination indicated that most abundant seedling species were associated with araucaria nurse plants, independent of seedling height class. Five of nine seedling species ≤ 50 cm tall, and four of six seedling species taller than 50 cm were associated with araucaria trees (Fig. 4). *Gordonia acutifolia*, a wind-dispersed forest species, was associated to araucaria nurse plants (Fig. 4A and B). Araucaria seedlings were mostly associated with *Baccharis uncinella* and *Pinus elliotti* nurse plants (Fig. 4A).

All of the more abundant seedling species presented vertebrate-dispersed diaspores. Except for *Araucaria angustifolia* and *Psidium cattleyanum*, which bear large diaspores, all other seedling species had small diaspores (Table 3). However, those large-sized diaspores were also dispersed by birds (L.S. Duarte, unpublished data, 2005). Among seedlings ≤50 cm tall, species lacking vertebrate dispersal agents represented 11% of total species number and only 4% of total abundance, and for taller seedlings, only 16.7% and 1.82%, respectively (Table 3).

Discussion

Our results show that isolated trees and shrubs established in *Campos* grassland promote the recruitment of forest woody species seedlings beneath their canopies. Other studies have drawn similar conclusions. Guevara *et al.* (1992), Slocum (2001) and Holl (2002) found more individuals of woody species under the canopy of isolated trees and shrubs than in the open field in a pasture. Furthermore, Nepstad *et al.* (1996) and Slocum and Horwitz (2000) demonstrated that isolated trees in pasture increase the arrival of forest species seeds, creating new forest colonisation sites. However, most studies deal with forest regeneration in degraded landscapes. Our study concerns forest expansion over natural grassland, in a naturally fragmented landscape (see also Scarano 2002). Archer *et al.* (1988) suggested a global tendency for increased woody plant abundance in grassland ecosystems, possibly caused by global climatic change or increased atmospheric CO_2 concentration (Bond & Midgley 2000). However, management practices should not be overlooked; the success of forest species establishment in a grassland matrix will depend on the disturbance regime (Pillar 2003).

Slocum (2001) found differences among tree species as nuclei for plant colonisation. Our results also indicate that shrub and tree seedlings of forest species colonising *Campos* grasslands are not randomly distributed beneath different isolated woody species. *Araucaria angustifolia* individuals growing isolated in natural grassland constitute major colonisation sites for forest woody species. Rigg *et al.* (2002) found that *Araucaria laubenfelsii* individuals scattered in maquis vegetation in New Caledonia facilitated establishment of rainforest woody species beneath their crowns. The authors found that *A. laubenfelsii* trees increased the retention of water by intercepting water from the atmosphere (cloud combing), thereby increasing soil moisture levels beneath their canopies in comparison to open areas. Additionally, saplings established beneath canopies of *A. laubenfelsii* suffered less photo-stress when compared to those occurring in open sites. Our study area experiences clouds and fog during long periods of the year, and possibly cloud combing plus shade protection also occurs beneath canopies of *Araucaria angustifolia* trees isolated in grassland. This remains to be tested. There is ecological similarity between *Araucaria laubenfelsii* in New Caledonia and *A. angustifolia* in South Brazil. Both species occur as emergent trees in forest and spread over open areas, acting as nurse plants for other forest woody species to establish, promoting forest expansion over grassland and/or shrubland. Also, both species occur in acidic, aluminium-rich soils and in sites under fire disturbance (Duarte *et al.* 2002; Rigg *et al.* 2002; Behling *et al.* 2004).

We found that most forest woody species colonising *Campos* grassland have small, red to black diaspores, suggesting an important role of birds as diaspore carriers from forest to grassland (Janson 1983; Howe & Westley 1988; Link & Stevenson 2004). Guevara *et al.* (1992) suggested that fleshy fruit-bearing nurse plants could be more attractive to birds than dry fruit-bearing trees. Thus, the former group could be more effective in concentrating diaspores beneath their canopy than the latter. Toh *et al.* (1999) tested this hypothesis but their results were not conclusive. We found that most seedling species were associated with araucaria trees, whose diaspores are an important food resource for birds and mammals. Possibly araucaria individuals attract more dispersers than other woody species established on grassland, increasing seed rain beneath their canopies. Furthermore, *Gordonia acutifolia*, a wind-dispersed species, was also associated with araucaria trees, suggesting that these nurse plants may provide more mesic conditions below their crowns, facilitating forest woody species establishment. The presence of *Araucaria angustifolia* individuals in grassland, whether as nurse plants or seedlings, also suggests the possible contribution of other vertebrate dispersal agents such as rodents in the process (Duarte *et al.* 2002), since araucaria seedlings were not associated with adults, indicating that those individuals were dispersed from another site to the grassland.

We propose two mechanisms to explain the success of *A. angustifolia* as nurse plant, as hypotheses to be confirmed or dismissed: First, *Araucaria angustifolia* trees ameliorate abiotic conditions for seedling establishment (Callaway 1995; Scholes & Archer 1997, Rigg *et al.* 2002). Callaway (1995) suggested that some species can play an important role as nurse plants by ameliorating microclimatic conditions (light, temperature, soil moisture and nutrients) beneath their canopies, and/or by altering the microbial soil community, including mycorrhyza, while others actively inhibit seedling establishment, for instance by allelopathy. Rigg *et al.* (2002) have already demonstrated that *Araucaria laubenfelsii* individuals ameliorate abiotic conditions and promote forest woody plant establishment below their canopies.

Second, the architecture of *Araucaria angustifolia* individuals may be more attractive to birds than other woody species in *Campos* grassland. According to Aukema and Martinez del Rio (2002), height and form of perches might have an influence on their use by birds. Our sampling indicates that *Araucaria* individuals are taller than other plant groups, and their crown area is greater. Further, they display straight, horizontally positioned branches, possibly more attractive to birds than denser canopies of other woody species. Thus, *A. angustifolia* trees may be good perches for frugivorous birds, increasing seed rain beneath their canopies. Several authors have stressed the major role played by nurse plants as perches for birds to rest and feed, thus increasing the seed rain below their crowns (Uhl 1987; Guevara *et al.* 1992; McClanahan & Wolfe 1993; Wunderle Jr. 1997; Toh at al. 1999; Galindo-González *et al.* 2000; Slocum & Horwitz 2000; Zimmerman *et al.* 2000; Aukema & Martinez-del Rio 2002; Holl 2002; Shiels &Walker 2003). Galindo-González *et al.* (2000) analysed the role of bats and birds in carrying seeds from forests to open pasturelands and concluded that isolated woody plants in pastures could possibly guide the movement of dispersers, "…determining the spatial deposition pattern of seeds in the landscape and developing 'nuclei of regeneration'… under isolated trees." Probably, these two mechanisms act synergistically.

Our results indicate that *Myrsine lorentziana* is the most abundant seedling species beneath nurse plants in the grassland. This species produces a large number of small, black, bird-dispersed drupes, mainly from October to January, when there are more frugivorous birds. Moreover, *M. lorentziana* is a fast-growing light-demanding species, and also reproduces vegetatively by means of root sprouting (J.M. Hermann 2004, unpublished data). Successful dispersal, associated with the tolerance of the species to stressful environmental conditions could explain the high abundance of *M. lorentziana* in grassland. Seedling establishment beneath nurse plants could be considered as the first step in establishing Araucaria Forest patches (so-called *capões*), commonly found mixed in the *Campos* grassland matrix, confirming Klein's (1960) ideas. Emerging questions suggested by our study concern the population dynamics of seedlings established beneath nurse plant canopies and the effect of disturbances by fire and grazing on seedling mortality rates. That is, under which circumstances would forest woody species seedlings in a grassland matrix generate a forest patch? Further studies are needed to answer this.

Finally, are our results a general trend that could be observed on *Campos* grassland? We think the answer is yes, since 1) Araucaria Forest expansion over grassland in Southern Brazil is largely demonstrated by paleopollen analysis (Behling *et al.* 2004), 2) Araucaria Forest patches surrounded by *Campos* grassland matrix are a common physiognomy of Northeastern Rio Grande do Sul highland plateau (Rambo 1994; Machado 2004), and 3) most forest shrubs and trees present in araucaria forests in the Northeast of Rio Grande do Sul possess animal dispersed diaspores (Kindel 2002). These three points suggest that the initial development of Araucaria Forest patches on *Campos* grassland, through the establishment of seedlings of forest woody species beneath nurse plants, must rely on vertebrate activity, especially of birds, which in this case most likely use *Araucaria angustifolia* isolated individuals in the grassland matrix as perches. Thus, the conservation of frugivorous vertebrate assemblages may help in maintaining 1) the potential for Araucaria Forest expansion over grasslands and 2) the regeneration of degraded Araucaria Forest sites. Myers *et al.* (2000) considered the Brazilian Atlantic Forest as one of five biodiversity hotspots internationally considered high priority for conservation efforts. However, these authors did not take into account the Brazilian Araucaria Forest in the priorities for conservation. We hope that increasing the number of research papers, with international coverage, concerned in exploring ecological patterns and processes involved in structure and dynamics of Brazilian Araucaria Forest, may bring more attention to this endangered ecosystem.

Acknowledgements

This study had logistic support from CPCN Pró-Mata PUCRS and was funded by research grants and fellowships from CAPES (project 005/02) and CNPq (projects 521472/95-4, 141810/2003-3). We are grateful to Gabriel S. Hofmann for field assistance. We thank Lázlo Orlóci, Fábio R. Scarano, Matthew Slocum, Amy Symstad, Karen Holl, Michael Bull and anonymous referees for helpful suggestions on the manuscript.

References

Archer S., Scifres C. & Bassham C. R. (1988) Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* **58**, 111-127.

Aukema J. E. & Martinez del Rio C. (2002) Variation in mistletoe seed deposition: effects of intra- and interespecific host characteristics. *Ecography* **25**, 139-144.

Backes A. (1999) Condicionamento climático e distribuição geográfica de *Araucaria angustifolia* (Bertol.) Kuntze no Brasil – II. *Pesquisas (Botânica)* **49**, 31-52.

Backes A., Fernandes A. V. & Zeni D. J. (2000) Produção de folhedo em uma floresta com *Araucaria angustifolia* no sul do Brasil. *Pesquisas (Botânica)* **50**, 97-117.

Behling H., Pillar V. D., Orlóci L. & Bauermann S. G. (2004). Late Quaternary *Araucaria* forest, grassland (*Campos*), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* **203**, 277-297.

Bond W. J. & Midgley G. F. (2000) A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**, 1–5.

Bruno J. F., Stachowicz J. J. & Bertness M. D. (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**, 119-125.

Callaway R. M. (1995) Positive interactions among plants. *The Botanical Review* **61**, 306-349.

Dalmagro A. D. & Vieira, E. M. (2005) Patterns of habitat utilization of small rodents in an area of Araucaria forest in Southern Brazil. *Austral Ecology* **30**, 353-362.

Duarte L. S. & Dillenburg L. R. (2000) Ecophysiological responses of *Araucaria angustifolia* (Araucariaceae) seedlings to different irradiance levels. *Australian Journal of Botany* **48**, 531-537.

Duarte L. S., Dillenburg L. R. & Rosa L. M. G. (2002) Assessing the role of light availability in the regeneration of *Araucaria angustifolia* (Araucariaceae). *Australian Journal of Botany* **50**,741-751.

Franco A. C. & Nobel P. S. (1989) Effect of nurse plants on the microhabitat anf growth of cacti. *Journal of Ecology* **77**, 870-886.

Galindo-González J., Guevara S. & Sosa V. J. (2000) Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology* **14**, 1693-1703.

Guevara S., Meave J., Moreno-Casasola P. & Laborde J. (1992) Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *Journal of Vegetation Science* **3**, 655-664.

Holl K. D. (2002) Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *Journal of Ecology* **90**, 179-187.

Howe H. F. & Smallwood J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* **13**, 201-228.

Howe H. F. & Westley L. C. (1988) *Ecological Relationships of Plants and Animals*. Oxford University Press, Oxford.

Hueck K. (1972) *As Florestas da América do Sul*. Ed. UnB- Ed. Polígono, São Paulo.

Janson C. H. (1983) Adaptation of fruit morphology to dispersal agents in a Neotropical Forest. *Science* **219**, 187-189.

Kindel A. (2002) *Diversidade e estratégicas de dispersão de plantas vasculares da floresta paludosa do Faxinal, Torres- RS*. Doctor Thesis, UFRGS, Porto Alegre.

Klein R. M. (1960) O aspecto dinâmico do pinheiro brasileiro. *Sellowia* **12**, 17-51.

Link A. & Stevenson P. R. (2004) Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia. *Revista Chilena de Historia Natural* **77**, 319-334.

Machado R. E. (2004) *Padrões vegetacionais em capões de floresta com araucaria no planalto nordeste do Rio Grande do Sul, Brasil*. MSc. Thesis, UFRGS, Porto Alegre.

Manly B. F. J. (1997) *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2^{nd} ed. Chapman and Hall, London.

McClanahan T. R. & Wolfe R. W. (1993) Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conservation Biology* **7**, 279-288.

Myers N., Mittermeier R. A., Mittermeier C. G., Fonseca G. A. B. & Kent J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403**, 853-858.

Nepstad D. C., Uhl C., Pereira C. A. & da Silva J. M. C. (1996) A comparative study of tree establishment in abandoned pasture and mature Forest of eastern Amazonia. *Oikos* **76**, 25-39.

Oliveira J. M. & Pillar V. D. (2004) Vegetation dynamics on mosaics of *Campos* and Araucaria forest between 1974 and 1999 in Southern Brazil. *Community Ecology* **5**, 197-202.

Oliveira-Filho A. T. & Fontes M. A. L. (2000) Patterns of floristic differentiation among atlantic forests in southeastern Brazil and the influence of climate. *Biotropica* **32**(4b), 793-810.

Pillar V. D. (1999) The bootstrapped ordination reexamined. *Journal of Vegetation Science* **10**, 895-902.

Pillar V. D. (2002) *SYNCSA - software for character-based community analysis*. Departamento de Ecologia, UFRGS, Porto Alegre. Software available from http://ecoqua.ecologia.ufrgs.br)

Pillar V. D. (2003) Dinâmica da expansão florestal em mosaicos de floresta e *Campos* no sul do Brasil. In: *Ecossistemas Brasileiros: Manejo e Conservação* (ed V. Claudino-Sales) pp. 209-216. Expressão Gráfica, Fortaleza.

Pillar V. D. (2004) *MULTIV - Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling; User's Guide v. 2.3.* Departamento de Ecologia, UFRGS, Porto Alegre. Software and manual available from http://ecoqua.ecologia.ufrgs.br)

Pillar V. D. & Orlóci L. (1996) On randomization testing in vegetation science: multifactor comparisons of relevé groups. *Journal of Vegetation Science* **7**, 585-592.

Rambo B. (1951) O elemento andino no pinhal riograndense. *Anais Botânicos do HBR* **3**, 7-39.

Rambo B. (1956) A flora fanerogâmica dos Aparados riograndenses. *Sellowia* **7** 235-298.

Rambo B. (1994) *A Fisionomia do Rio Grande do Sul*. 3rd ed., Ed. Unisinos, São Leopoldo.

Rigg L. S., Enright N. J., Perry, G. L. W. & Miller B. P. (2002) The role of cloud combing and shading by isolated trees in the succession from maquis to rain forest in New Caledonia. *Biotropica* **34**(2), 199-210.

Sankaran M., Ratnam J. & Hanan N. P. (2004) Tree–grass coexistence in savannas revisited – insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters* **7**, 480–490.

Scarano F. R. (2002) Structure, function and floristic relationships of plant communities in stressful habitats marginal to the Brazilian Atlantic Rainforest. *Annals of Botany* **90**, 517-524.

Scholes R. J. & Archer S. R. (1997) Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* **34**, 575-604.

Shiels A. B. & Walker L. R. (2003) Bird perches increase forest seeds on Puerto Rican landslides. *Restoration Ecology* **11**, 457-465.

Slocum M. G. (2001) How tree species differ as recruitment foci in a tropical pasture. *Ecology* **82**, 2547-2559.

Slocum M. G. & Horwitz C. C. (2000) Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecology* **149**, 51-62.

Tabarelli M. & Peres C. A. (2002) Abiotic and vertebrate seed dispersal in the Brazilian Atlantic Forest: implications for forest regeneration. *Biological Conservation* **106**, 165-176.

Tewksbury J. J. & Lloyd J. D. (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* **127**, 425-434.

Toh I., Gillespie M. & Lamb D. (1999) The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restoration Ecology* **7**, 288-297.

Uhl C. (1987) Factors controlling succession following slash-and-burn agriculture in Amazonia. *Journal of Ecology* **75**, 377-407.

Waechter J. L. (2002) Padrões fitogeográficos na flora atual do Rio Grande do Sul. *Ciência & Ambiente* **24**, 93-108.

Wunderle Jr. J. M. (1997) The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* **99**, 223-235.

Zimmerman J. K., Pascarella J. B. & Aide T. M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology* **8**, 350-360.

Table 1. Isolated woody plants sampled on *Campos* grassland area, São Francisco de Paula, RS, South Brazil. N refers to number of sampled individuals. † Standard errors.

Nurse plant species	Botanical family	N	Mean plant height ± SE † (m)	Total crown area (m^2)
Baccharis uncinella DC.	Asteraceae	63	1.97 ± 0.03	272.18
Pinus elliotti Engelm.	Pinaceae	12	3.88 ± 0.28	63.20
Myrceugenia euosma (O. Berg.) D. Legrand	Myrtaceae	8	2.17 ± 0.11	36.21
Araucaria angustifolia (Bertol.) Kuntze	Araucariaceae	6	6 ± 0.97	207.90
Baccharis mesoneura DC.	Asteraceae	5	2 ± 0.13	12.68
Others:		6	2.28 ± 0.21	14.47
Agarista eucalyptoides G. Don.	Ericaceae			
Agarista nummularia G. Don.	Ericaceae			
Croton tenuissimus Daill.	Euphorbiaceae			
Myrsine lorentziana Arech.	Myrsinaceae			
Miconia hyemalis A. St.-Hil. & Naud. ex Naud.	Melastomataceae			
Psidium cattleyanum Weinw.	Myrtaceae			
Total		100		606.64

Table 2. Seedling density (individuals per m^2) beneath isolated trees and shrubs sampled on *Campos* grassland, São Francisco de Paula, South Brazil.

Seedling species	Botanical Family	Mean density	%	Vertebrate dispersed?
≤50 cm height				
Myrsine lorentziana Arech.	Myrsinaceae	0.119	69.90	Yes
Miconia hyemalis A. St.-Hil. & Naud. ex Naud.	Melastomataceae	0.013	7.77	Yes
Araucaria angustifolia (Bertol.) Kuntze	Araucariaceae	0.007	3.88	Yes
Gordonia acutifolia (Wawra) H. Keng.	Theaceae	0.007	3.88	No
Siphoneugena reitzii D. Legrand	Myrtaceae	0.007	3.88	Yes
Ilex dumosa Reissek	Aquifoliaceae	0.007	3.88	Yes
Psidium cattleyanum Weinw.	Myrtaceae	0.002	0.97	Yes
Other Myrtaceae		0.008	4.85	Yes
Ilex microdonta Reissek	Aquifoliaceae	0.002	0.97	Yes
Total		0.170	100.00	
> 50 cm height				
Myrsine lorentziana Arech.	Myrsinaceae	0.077	83.93	Yes
Siphoneugena reitzii D. Legrand	Myrtaceae	0.008	8.93	Yes
Ilex dumosa Reissek	Aquifoliaceae	0.002	1.79	Yes
Miconia hyemalis A. St.-Hil. & Naud. ex Naud.	Melastomataceae	0.002	1.79	Yes

Table 2. Cont.

Ilex microdonta Reissek	Aquifoliaceae	0.002	1.79	Yes
Gordonia acutifolia (Wawra) H. Keng.	Theaceae	0.002	1.79	No
Total		0.092	100.00	

Table 3. Diaspore length size of vertebrate-dispersed seedlings on *Campos* grassland, São Francisco de Paula, South Brazil.

Seedling species	Mean diaspore size (mm)	Diaspore size class	Diaspore color
Araucaria angustifolia	55.0	Large	Brown
Ilex dumosa	5.0	Small	Dark
Ilex microdonta	5.0	Small	Red, purple, dark
Miconia hyemalis	3.0	Small	Dark
Myrsine lorentziana	3.4	Small	Dark
Psidium cattleyanum	28.0	Large	Yellow, red
Siphoneugena reitzii	5.5	Small	Red, purple

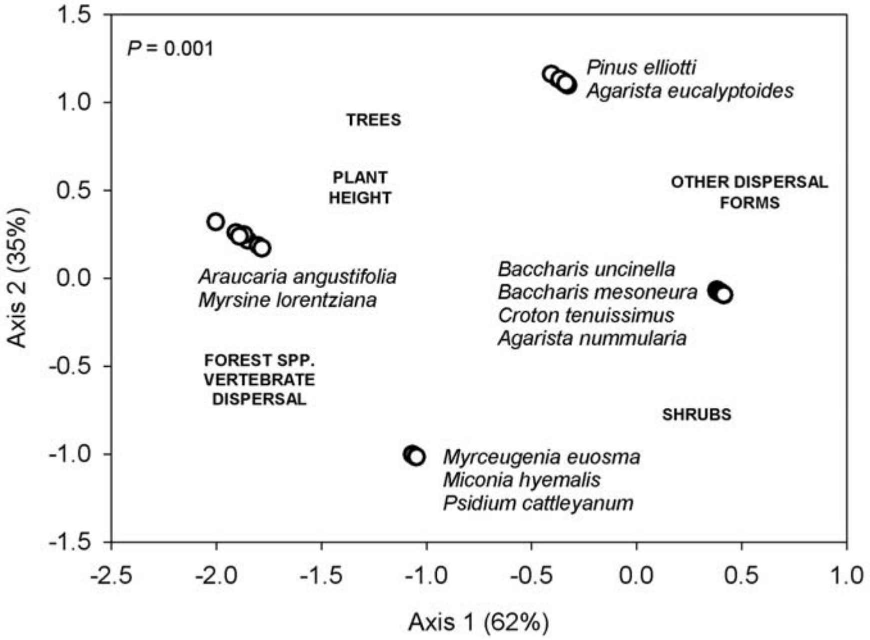

Fig. 1. *Ordination diagram from principal coordinates analysis of isolated woody plants in* Campos *grassland, São Francisco de Paula, RS, South Brazil.* P*-value for stability of axes generated by bootstrap auto-resampling (1,000 bootstrap samples).*

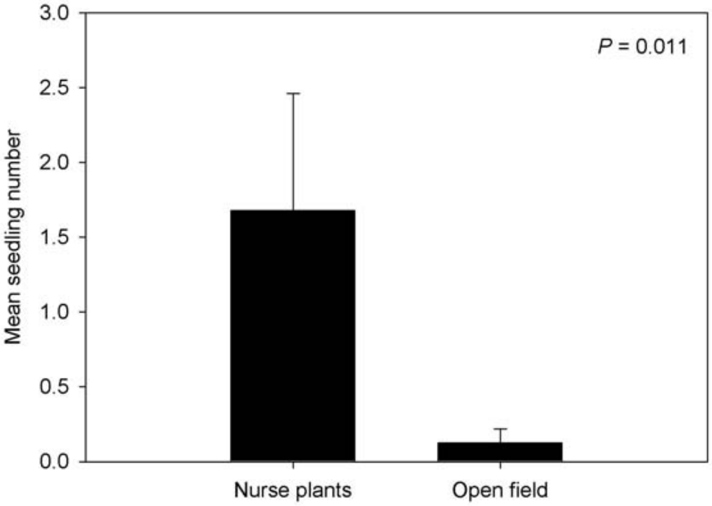

Fig. 2. *Seedling number beneath nurse plants and on open sites at* Campos *grasslands, São Francisco de Paula, RS, South Brazil. Vertical line above bar indicate standard errors. N = 192.* P-*value generated by randomization testing (10,000 random permutations).*

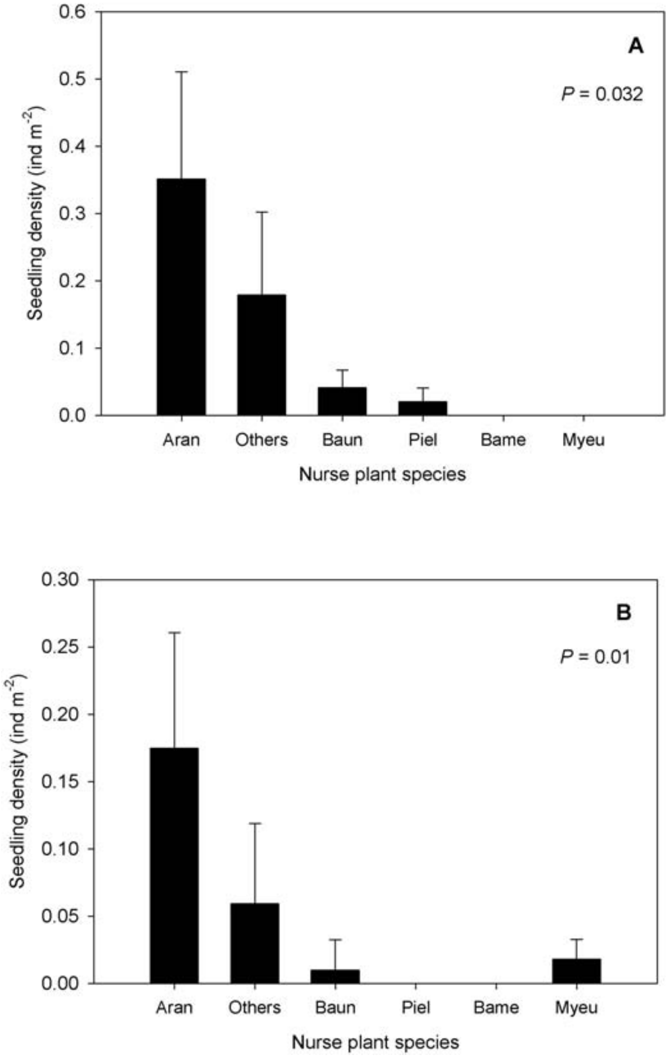

Fig. 3. *Seedling density beneath nurse plants in* Campos *grassland, São Francisco de Paula, RS, South Brazil. A – plants ≤ 50 cm height; B – plants > 50 cm height. Species name abbreviation referred at Table 1. N = 97.* P *values originated from orthogonal contrast comparison between* Araucaria angustifolia *group and all other groups (10,000 random permutations).*

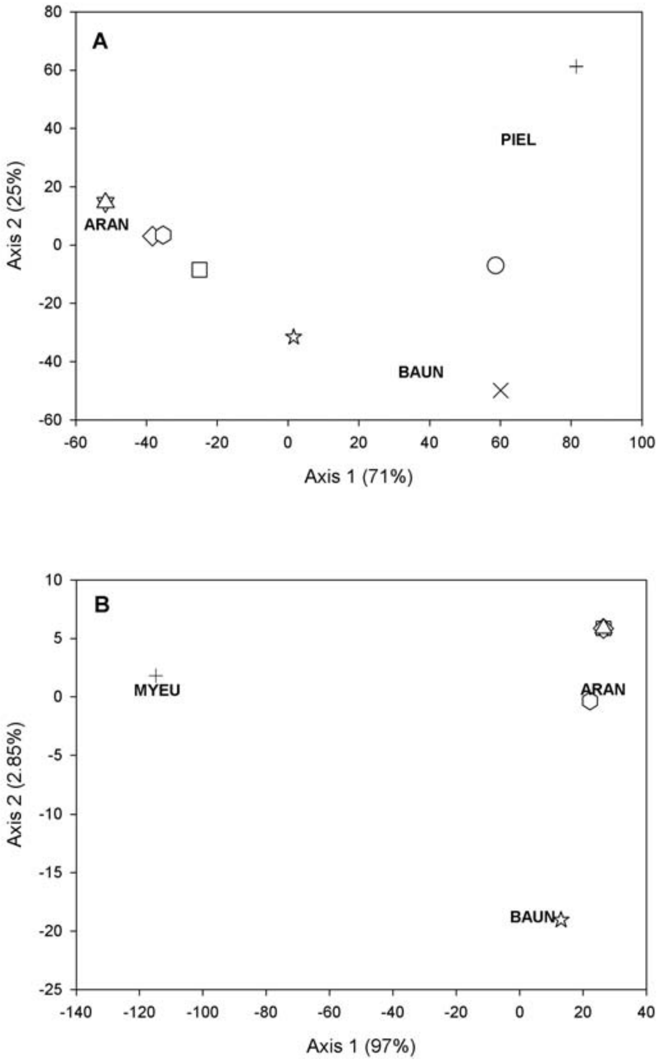

Fig. 4. *Ordination diagram from principal coordinates analysis of seedling species established beneath nurse plant crowns in* Campos *grassland, São Francisco de Paula, RS, South Brazil. A – seedlings ≤ 50 cm height, B – seedlings > 50 cm height. Seedling symbols -* ***Triangle up****:* Gordonia acutifolia*;* ***triangle down****:* Psidium cattleyanum*;* ***square****:* Ilex dumosa*;* ***cross****:* Ilex microdonta*;* ***circle****:* Araucaria angustifolia*;* ***X****: Myrtaceae;* ***star****:* Siphoneugena reitzii*;* ***hexagon****:* Myrsine lorentziana*;* ***diamond****:* Miconia hyemalis. *Nurse plant codes -* ***ARAN****:* Araucaria angustifolia*;* ***BAUN****:* Baccharis uncinella*;* ***MYEU****:* Myrceugenia euosma*;* ***PIEL****:* Pinus elliotti.

Capítulo 3. What saplings can tell us about forest expansion over natural grasslands[2]

Duarte, Leandro da S.[*]; Machado, Rafael E.[1]; Hartz, Sandra M.[2] & Pillar, Valério D.[3]

Departamento de Ecologia, Universidade Federal do Rio Grande do Sul CP 15007, Porto Alegre, RS 91501-970, Brazil; [1]E-mail xmachadox@terra.com.br; [2]E-mail hartzsm@ecologia.ufrgs.br; [3]E-mail vpillar@ecologia.ufrgs.br

*Corresponding author; Fax 0055-51-33167626; E-mail lsduarte@ecologia.ufrgs.br

Resumo

Questões: 1. A composição de espécies, riqueza e diversidade de comunidades de plantas jovens varia significativamente em manchas de tamanhos diferentes? 2. Manchas florestais de tamanhos diferentes diferem nos padrões de colonização por plantas lenhosas?

Local: São Francisco de Paula, Rio Grande do Sul, Brasil, 29°28' S, 50°13' W.

Métodos: Três tipos de vegetação lenhosa, diferindo em desenvolvimento estrutural (tamanho da mancha) e recuperando há 10 anos de distúrbio por criação de gado e queimadas, foram amostrados no campo. Nós analisamos a composição e complexidade das comunidades de indivíduos lenhosos jovens, através de padrões de abundância relativa, riqueza e diversidade. Nós também avaliamos o status de recrutamento (residentes vs. colonizadoras) de espécies em comunidades ocorrendo em manchas de diferentes classes de tamanho.

---

[2] Artigo publicado no periódico *Journal of Vegetation Science* (2006) 17:799-808.

Resultados: 1. Há um gradiente de composição nas comunidades de plantas jovens fortemente associado com a área da mancha florestal. 2. A riqueza e a diversidade são positivamente correlacionadas com a área da mancha, mas somente em manchas pouco estruturadas; manchas grandes apresentam valores de riqueza e diversidade similar às manchas pequenas. 3. A razão entre a abundância de residentes e colonizadoras aumenta de plantas-berçário para manchas grandes. A proporção do número de espécies entre residentes a colonizadoras é similar em manchas pequenas e grandes. 4. Manchas grandes apresentaram um alto número de espécies exclusivas, enquanto plantas-berçário e manchas pequenas não.

Conclusões: Comunidades de plantas lenhosas na floresta com *Araucaria* estão associadas ao desenvolvimento estrutural das manchas. Padrões de riqueza e diversidade estão ligados aos padrões de colonização das manchas. Espécies generalistas colonizam o sub-bosque de plantas-berçário e manchas pequenas; espécies residentes não podem recrutar muitos novos indivíduos. Em manchas grandes, o recrutamento de indivíduos jovens por adultos residentes inibe a imigração de novas espécies para as manchas, limitando a riqueza e a diversidade.

Palavras-chave: Floresta com *Araucaria*; Campos; Diversidade; Nucleação;
Ecossistema em manchas; Comunidade de plantas jovens.

Abstract

Question: 1) Do the species composition, richness and diversity of sapling communities vary significantly in differently sized patches? and 2) Do forest patches of different sizes differ in woody plant colonization patterns?

Location: São Francisco de Paula, Rio Grande do Sul, Brazil, at about 29°28'S and 50°13'W.

Methods: Three woody vegetation types differing in structural development (patch size) and recovering for 10 years from cattle and burning disturbances were sampled on grassland. We analyzed the composition and complexity of the forest woody sapling communities, through relative abundance, richness and diversity patterns. We also evaluated recruitment status (residents vs. colonizers) of species in communities occurring in different forest patch size classes.

Results: (1) There is a compositional gradient in sapling communities strongly associated with forest patch area. (2) Richness and diversity are positively correlated to patch area, but only in poorly structured patches; large patches present richness and diversity values similar to small patches. (3) Resident to colonizer abundance ratio increases from nurse plants to large patches. The species number proportion between residents and colonizers is similar in small and large patches, and did not differ between these patch types. (4) Large patches presented a high number of exclusive species, while nurse plants and small patches did not.

Conclusions: Woody plant communities in *Araucaria* Forest patches are strongly associated with patch structural development. Richness and diversity patterns are closely linked to patch colonization patterns. Generalist species colonize nurse plant understories and small patches, where resident species are unable to massively recruit new individuals. In large patches, sapling recruitment by resident adults precludes the immigration of new species into the patches, limiting richness and diversity levels.

Keywords: *Araucaria* Forest, *Campos* grasslands, sapling communities, nucleation, patchy ecosystems.

Nomenclature: APG (2003); Anon. (2005)

Introduction

Vegetation dynamics is a central issue in the ecological agenda (Cook et al. 2005). Direct periodic observation of vegetation change by means of permanent plots is the most accurate way to analyze community dynamics. Unfortunately, this approach is not always possible, especially in poorly studied environments. In those cases, static models can represent functional tools for understanding general patterns in vegetation dynamics (Pickett 1989; Cook et al. 2005). Community development is a result of structural variation along time. Pickett (1989) stressed the importance of the operational environment, i.e. the set of conditions and interactions that control system behavior, in community dynamics modeling. In this context, knowledge on recovery patterns of communities released from disturbance regimes can be useful in order to understand long-term processes.

Forests with *Araucaria angustifolia* constitute the main forest type on the highland plateau in South Brazil at altitudes above 500 m a.s.l. (Hueck 1972; Duarte & Dillenburg 2000). These forests often form mosaics with *Campos*, which is a natural type of grassland (Rambo 1994; Duarte et al. 2002). *Araucaria* Forest expansion over grassland in southern Brazil is largely demonstrated by paleopollen evidence (Behling 2002; Behling et al. 2004). According to Behling et al. (2004), a change from a drier to a moister climate that occurred 4300 yr BP favored *Araucaria* Forest expansion, especially in the last millennium. Nowadays, these forests can naturally expand over grassland (Rambo 1956; Klein 1960; Hueck 1972; Oliveira & Pillar 2004). However, burning and domestic cattle grazing have likely slowed down or stopped the process (Pillar 2003; Machado 2004). In areas where cattle are extensively raised, herds use *Araucaria* Forest patches as shelter, browsing and trampling the forest floor inside patches and thus preventing forest regeneration; cattle exclusion from forest patches allows successful forest species recruitment (personal observation).

Araucaria Forest expansion over *Campos* grassland occurs gradually by edge dynamics (Oliveira & Pillar 2004), or by nucleation (sensu Yarranton & Morrison 1974) of forest patches in the grassland (Klein 1960; Duarte et al. 2006). Recently we demonstrated the importance of shrubs and trees (particularly *Araucaria angustifolia*) in the initial establishment of forest species on grassland (Duarte et al. 2006). Nucleation is a process obviously related to area effects (Archer et al. 1988; Cabral et al. 2003, Cook et al. 2005). However, major mechanisms involved in forest patch dynamics remain unknown. In fact, Cook et al. (2005) pointed out the lack of knowledge about the influence of habitat area on community dynamics. According to the Equilibrium Theory (MacArthur & Wilson 1967), patch expansion should result in increased species richness. More recently, the Unified Neutral Theory of Biodiversity and Biogeography (UNTBB) (Hubbell 2001) stated that the area effect acts on the maximum number of individuals supported by the habitat rather than directly on the species number. Furthermore, as a forest patch expands, the capacities of plant species to tolerate environmental conditions and to explore the resources should vary (Connell & Slatyer 1977; Tilman 1996; Tilman 2004). According to Cook et al. (2005), patch area is expected to be associated with major successional trends, since larger patches tend to present more accelerated ecological dynamics than smaller patches.

In this study we analyzed sapling recruitment patterns in *Araucaria* Forest patches varying in area and scattered on a *Campos* grassland site where grazing and fire disturbances have been suppressed for ca. 10 years. Since all patches had the same time of recovery from disturbance, differences between patches in relation to vegetation recruitment patterns were expected to reveal the effect of structural development variation on post-disturbance vegetation dynamics. Our focus was on sapling communities, which are good indicators of dynamic trends of the forest woody plant communities, since they represent the net result of recent dynamics at a given site and indicate how that community is going to be in the near future. We address the following questions: 1) Do the species composition, richness and diversity of sapling communities vary significantly in differently sized patches? and 2) Do forest patches of different sizes differ in woody plant colonization patterns?

Material and Methods

Study area

The study was conducted at the Pró-Mata Research and Nature Conservation Center (CPCN Pró-Mata). The Center has a 4 500 ha area, in the town of São Francisco de Paula (29°28'S and 50°13'W), Rio Grande do Sul State, southern Brazil. The study site was on a plateau at ca. 900 m a.s.l. (Machado 2004; Oliveira & Pillar 2004), and consisted of approximately 78 ha *Campos* grassland surrounded by *Araucaria* Forest, in which several small forest patches occur scattered throughout the area. The climate is classified according to the Köppen system as Cfb (Dalmagro & Vieira 2005). The annual mean temperature is ca. 14.5°C, with negative temperatures occurring from April to November (Backes 1999), and the annual mean rainfall is 2 252 mm, with high rainfall levels occurring every month (Backes et al. 2000). The presence of species phytogeographically related to Austral-Antarctic and Andean floras distinguish *Araucaria* Forest communities from more tropical facies of Brazilian Atlantic forests (see Rambo 1951; Waechter 2002). The most physiognomically important tree species is *Araucaria angustifolia*. Some other typical species found in those forests are *Podocarpus lamberti*, *Drimys brasiliensis*, *Dicksonia sellowiana*, and several species of Myrtaceae, Melastomataceae and Lauraceae. Cattle grazing and burning practices were terminated since

1994, allowing increasing regeneration in the forest and more biomass accumulation and woody plant establishment in the grasslands (Oliveira & Pillar 2004).

Sampling Methods

Forest patches occurring in the grassland matrix were classified in three size classes representing different structural development stages:

Nurse plants (see Plate 1a): Duarte et al. (2006) demonstrated that *Araucaria angustifolia* individuals are preferential sites for sapling establishment on grassland. Thus, we sampled all isolated *Araucaria* trees in the grassland site, considering isolated any tree occurring without any neighbor tree or tall shrub touching its crown. Crown cover was taken as the patch size and was estimated from crown projection diameter (Table 1). All forest woody saplings occurring beneath tree canopy were counted and identified, and the relative cover of each species was visually estimated using the Braun-Blanquet cover scale (Braun-Blanquet 1979). We sampled 26 *Araucaria* trees from October to December 2003; two individuals were ignored since no sapling was found beneath their canopies.

Small patches (see Plate 1b): They represented an intermediate stage of structural development, between nurse plants and large patches. We defined as forest patch any group of forest woody plants with at least one adult tree and accompanying shrubs, forming a continuous canopy, surrounded by a continuous herb layer (Krebs 2001; Cabral et al. 2003). We considered a small patch any forest woody vegetation lacking a clear vertical structure, generally with few adult trees and a variable amount of woody saplings. The canopies were considerably open, allowing grassland species to resist to some extent to forest invasion. We estimated the total patch area as an ellipse, using the maximum length and maximum width of the patch canopy (Table 1). From January to February 2005, we sampled 10 small patches. All forest woody individuals ≥ 5 cm in diameter at breast height (DBH) were counted and identified, and the relative cover of each species was estimated from the basal area (Mueller-Dombois & Ellenberg 1978). Along the main axis of each patch we delimited 1.7 m x 1.7 m quadrats, within which all forest woody individuals <5 cm DBH were counted and identified; the relative cover of each species was visually estimated using Braun-Blanquet's cover scale. We surveyed on average five quadrats per sampling unit, which represented eight percent of the total area of the small patches (Table 1).

Large patches (see Plate 1c): We used data available from Machado (2004), who sampled 5 large forest patches in the grassland matrix between 2002 and 2003 (Table 1). These patches presented high structural development when compared to nurse plants and small patches, since they had a structured tree layer, a well-defined shrub layer, and a herb layer consisting exclusively of forest species. The author used 5 m x 5 m quadrats to sample woody individuals ≥ 5 cm DBH, and small quadrats (1.7 m x 1.7 m) delimited within larger quadrats to sample individuals <5 cm DBH. Relative cover of species was visually estimated using Braun-Blanquet's cover scale. Since our interest was only on forest woody species, we ignored non-forest species and recalculated relative abundances based only on forest species. We surveyed on average 72 quadrats per sampling unit, which accounted for 11% of the total area of the large patches (Table 1).

In order to verify whether any bias in the analyses would arise from the fact that small forest patches were surveyed 1-2 years later than nurse plants and large forest patches, we used additional data on the sapling community structure beneath the same nurse trees, which were re-surveyed in 2005 at the same time as the small forest patches (L.S. Duarte unpublished data). We computed Euclidean distances between nurse trees in October-December 2003 and similar distances between the same nurse trees in January-February 2005. We performed a Mantel test (Mantel 1967) for the correlation between these two matrices ($r = 0.37$) and found it highly significant ($P << 0.01$), which indicates similar sapling community structure beneath the nurse trees in both years. Therefore, the comparison between nurse trees and small forest patches was not biased. By extension, we assumed that large patches were similarly stable at this time scale.

We described each sampling unit by the abundance of forest woody saplings, i.e., species dispersed from the surrounding forest. For this we measured a relative abundance index (RAI), computed from the relative frequency (RF) and relative cover (RC):

$$RAI(\%) = \frac{(RF + RC)}{2}$$

In this way a data matrix describing communities (sampling units) by the relative abundances of sapling species (variables) was used for the analyses.

To analyze the recruitment status of each species, individuals ≥ 5 cm and < 5 cm DBH were assembled in two size classes, respectively, as presumed adult tree-shrubs (hereafter simply called *adults*) and as saplings. For each species in each patch size class (nurse plants, small patches and large patches) we counted (a) the number of sampling units with co-occurrence of adults and saplings of the species and (b) the number of sampling units with occurrence only as adults or (c) only as saplings; and then a Jaccard similarity index was computed as $J = a/(a+b+c)$. To be considered *resident* in a given patch size class, a species must be present in both adult and sapling classes in at least one sampling unit ($J > 0$). Species present only as saplings, or not occurring simultaneously in the same units as saplings and adults, were considered *colonizers*. Species occurring only as adults in the same patch size class were considered *non-recruiter* species. Thus, for each patch size class, we obtained a set of residents, colonizers and non-recruiters. Undetermined species were removed from the analyses.

Data Analyses

We carried out a Principal Coordinates Analysis (PCoA) of sampling units in order to detect the principal axes of variation of sapling communities and their association with patch size. The data were previously log-transformed and the ordination was based on Euclidean distances between sampling units. Stability of the ordination axis was evaluated through bootstrap resampling (Pillar 1999). Additionally, we analyzed the association between the main axes of PCoA scores and the patch size through linear regression analysis (Sokal & Rohlf 1981). For this analysis we used the residuals of a regression of PCoA scores on the surveyed area, instead of the original scores themselves, since there was a significant positive correlation between patch size and sampling effort ($r = 0.89$, $P << 0.01$). This procedure allowed us to remove the effect of varying sampling effort in different patch size classes.

We evaluated the complexity of sapling communities for each sampling unit using richness and diversity indexes, based on the Rényi generalized entropy formula (see Anand & Orloci 1996):

$$H_\alpha(S) = \frac{1}{1-\alpha}\log_2 \sum_{j=1}^{q} p_j^\alpha, \text{in bits}$$

where q indicates the number of components (species) of the system S (community), p_j is the proportion of the species j in the community and α is the order of entropy. Most frequently used diversity indexes, like Shannon's, are special cases of Rényi entropy. When α tends to 1, Rényi entropy equals Shannon's entropy. When $\alpha = 0$, the entropy value does not take into account the variation in the proportion of different species in a given community, and behaves as a richness index. Anand & Orlóci (1996) pointed out that the effect of varying species p (the equitability effect) is only stabilized when an order of entropy much higher than Shannon's ($\alpha \cong 1$) is used, and suggested $\alpha = 12$ as a good entropy order. Thus, we adopted the entropy orders 0 and 12 for richness and diversity analysis, respectively.

In order to evaluate the association between richness (or diversity) and patch size, we also used the residuals of a regression of richness (or diversity) on the surveyed area, to remove the effect of the sampling effort. Based on these residuals we computed Euclidean distances between sampling units, in order to verify differences in richness and diversity between the patch size classes. For this we used an analysis of variance with randomization testing, using sum of squares between groups (Qb statistics) as the test criterion (Pillar & Orloci 1996). In the cases when analyses of variance indicated significant differences between groups, we performed contrast analyses to verify which groups differed from others (Pillar & Orloci 1996). The significance of contrasts was evaluated through randomization, in a similar way as in the variance analyses (Pillar & Orloci 1996). The same approach was used to evaluate the differences between the mean abundance and the mean species number proportion of resident and colonizer species in different forest patch classes.

Regression analyses were carried using the SigmaStat 3.11 software (Systat Software Inc. 2004). All other analyses were performed using the MULTIV 2.3.17 (Pillar 2004) statistical software.

Results

A detailed description of sapling communities is available in Table 2. Undetermined species removed from analyses (taxonomic noise) represented less than 1% of the total variance in each vegetation type (Table 2). We found a species pool common to all patch size classes, constituted by nine species, namely *Araucaria angustifolia*, *Drimys brasiliensis*, *Gordonia* *acutifolia*, *Ilex microdonta*, *Lamanonia ternata*, *Miconia hyemalis*, *Myrsine lorentziana*, *Psidium cattleyanum* and *Siphoneugena reitzii*. This species group accounted for 91% of relative abundance beneath *Araucaria* nurse plants. In small patches and large patches, those species still remained with, respectively, 69% and 59% of relative abundance (Table 2). Moreover, they represented 43% of species in small patches and 18% in large patches (Table 2). Nurse plants did not present any exclusive species beneath their canopies, while small patches presented just one species (Table 3). On the opposite side, large patches presented 33 exclusive species. Most of the exclusive species found in large patches was constituted by colonizers (Table 3).

Ordination analysis of sapling communities indicated a significant gradient along the first ordination axis (Fig. 1). While lower scores were associated with *Araucaria* nurse trees, higher scores were related to large patches. Small patches had an oscillating distribution; while some small patches were positioned close to the nurse plants, others showed greater proximity to large patches. This gradient along the first ordination axis was characterized by an increase in *Myrcia retorta*, *M. guianensis*, *Drimys brasiliensis*, *Daphnopsis fasciculata*, *Miconia cinerascens*, *Siphoneugena reitzii*, *Vernonia discolor* and *Ilex microdonta*. Those species were more abundant in large patches. Regression analysis indicated a significant association between patch area and the first axis scores of PCoA, after accounting for the effect of sampling effort (Fig. 2).

Small and large patches presented higher richness and diversity mean values than nurse plants; however, they did not differ from each other, after accounting for the effect of sampling effort (Fig. 3). Beneath *Araucaria* nurse plants, sapling communities were constituted mostly by colonizer species, both in abundance and species number proportion terms (Fig 4a and b). Large patches presented the highest abundance of resident species and the lowest abundance of colonizers, while small patches had intermediary values between nurse plants and large patches

(Fig. 4a). Nonetheless, small and large patches did not differ in relation to the proportions of resident and colonizer species (Fig. 4b).

Discussion

Our study indicated that the recruitment of woody saplings in *Araucaria* Forest patches released for ten years from a secular disturbance regime was strongly associated with the structural development of the patches. We observed a positive relationship between patch area and species richness, a result very similar to other studies (e.g. Archer et al. 1988; Cabral et al. 2003; Cook et al. 2005). However, this pattern was only evident when we compared *Araucaria* nurse plants with small and large patches. Despite large patch areas being approximately ten times larger than small patches, richness and diversity did not differ significantly between those patch types, which is contrary to the classical species-area positive association (MacArthur & Wilson 1967). The UNTBB (Hubbell 2001) states that species richness is a function of the maximum number of individuals (J) supported by a given habitat patch (the zero-sum dynamics). Since J is spatially dependent on the patch size, the UNTBB prediction is that large patches must present higher species richness than small patches, which was not observed. Unfortunately, we did not have any information on the carrying capacity of the patches, and then we could not evaluate zero-sum dynamics in the present study. Nonetheless, the UNTBB also predicts that whenever a habitat patch comes closer to its specific J value, the probability of any dead individual being replaced by a new immigrant species (m) must decrease. Nucleation dynamics involves the increased recruitment of new individuals by mature resident species (Yarranton & Morrison 1974; Cook et al. 2005). The more intense is this process, more rapidly the number of individuals in the patch should tend to J, and patch colonization by new species must be progressively prevented as *m* decreases (see Fargione et al. 2003). Thus, richness patterns observed in this study probably reflected differences between patches in respect to their receptiveness for colonizer species. Post-disturbance colonization by new species was favored beneath *Araucaria* nurse plants and in small patches, when compared to large patches, since nurse plants and small patches had few adult plants capable to recruit new individuals (high *m* probability). Instead, large patches possessed well-structured shrub/tree communities, making possible the intense recruitment of new individuals by resident species, and precluding a more pronounced establishment of new colonizers (low *m* probability).

We found that small and large patches had similar diversity values. However, the components of diversity were distinct when we compared small and large patches. In small patches, colonizer species were more abundant than in large patches, which contributed to the increase of diversity. The low abundance of colonizers in large patches pulled down diversity values, although both patch types presented a similar species number proportion of residents and colonizers (close to a 1:1 ratio), which suggested that the colonization by new species was not limited by seed dispersal from continuous forest. Anjos & Boçon (1999) found a positive association between *Araucaria* Forest patch area and the number of frugivorous bird species present in the patches. Thus, a more pronounced seed rain in the well-structured large patches might be expected, since those patches have more appeal to a large amount of vertebrate dispersers than the poorly structured nurse plants and small patches. Disperser attraction might possibly counterbalance the negative effect of resident recruitment.

According to the Stochastic Niche Theory (SNT) proposed by Tilman (2004), the colonization of forest patches by immigrant species might be explained by a niche-based mechanism, in which the probability of a colonizer to survive until maturity depends on its capacity to explore the resources left available by the resident species. In other words, colonizers must not show overlapping niche characteristics related to establishment with resident populations. In this study we found that most species established beneath *Araucaria* nurse plants were also abundant in small and large patches. Those generalist species occurred in a broad set of environmental conditions, from the very open and grassy understory of *Araucaria* nurse plants to the darker understory of large patches. In small and large patches, they accounted for a considerable part of resident sapling populations. Our results showed that in small patches, where resident saplings were less abundant than in large patches, colonizer sapling communities were constituted mainly by generalist species. In large patches, more than 90% of relative abundance was constituted by resident saplings of generalist species. Nonetheless, most colonizers were exclusive species, totally absent in poorly structured patches. If colonizers presented distinct ecological requirements in relation to resident species, we could hypothesize that SNT was also operating in nucleation dynamics. Perhaps woody species colonizing large patches allocate more energy to seed reserves than those generalist species, in order to be more competitive and successfully occupy the few spaces left by the residents (Foster & Janson 1985; Moles & Westoby 2004). A large amount of evidences indicate that seed size/number ratio represent an important trade-off for plants, being closely associated with differential capacities of survival (investment in reserves) or dispersal (investment in seed number) of the species, across a vast variety of habitats (Leishman 2001; Leishman & Murray 2001; Moles & Westoby 2004). It remains to be tested.

We live in a changing world, where a global tendency for increased woody plant abundance on grasslands ecosystems has been suggested (Archer et al. 1988). Nonetheless, studies focusing on forest nucleation in grassland landscapes are scarce, especially in less developed countries. Brazilian *Araucaria* Forest is one of the most threatened (and less known) ecosystems in South America. *Araucaria angustifolia* itself is nowadays considered a threatened species (Hilton-Taylor 2000). Thus, ecologists focused on this marvelous landscape must use approaches that optimize the evaluation of environmental processes and mechanisms involved in its structure and dynamics in short-term studies. Nucleation is a very complex phenomenon, and long-term monitoring studies on *Araucaria* Forest sites are lacking. Thus, static models should be used as functional tools for understanding ecological patterns in this ecosystem (see Pickett 1989). Besides, we also need proposing long-term studies in order to confirm or dismiss the hypotheses generated by static models. According to the scenario above described, what saplings can tell us about forest dynamics? First, sapling dynamics represent an excellent tool to study forest dynamics, since sapling communities show how the present community is working, and how the near-future community is going to work. Our study showed the major trends in woody plant colonization in *Araucaria* Forest patches varying in structural development and recovering from secular disturbance. Second, working with saplings instead adults is less time-consuming. This point is very important for studies with conservation purposes. Last, but not least, our methodological approach raised some important questions about the ecological mechanisms underlying forest patch colonization: Are colonizer species ecologically distinct from the residents? Seed dispersal by vertebrates affects plant colonization in forest patches? We hope to answer these and other questions in future studies.

Acknowledgements

This study had logistic support from CPCN Pró-Mata PUCRS and was funded by research grants and fellowships from CAPES (project 005/02) and CNPq (project 141810/2003-3). The authors thank Andreas Kindel, Helge Bruelheide and Hermann Behling for helpful suggestions on the manuscript.

References

Anand, M. & Orlóci, L. 1996. Complexity in plant communities: the notion and quantification. *J. Theor. Biol.* 179: 179-186.

Anjos, L. & Boçon, R. 1999. Bird communities in natural forest patches in Southern Brazil. *Wilson Bull.* 111: 397-414.

Anon. 2004. *SigmaStat for Windows v. 3.11*. Richmond, VI, USA.

Anon. 2005. *The International Plant Names Index*. URL: http://www.ipni.org [accessed from March to August 2005].

APG 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399-436.

Archer, S., Scifres C. & Bassham C. R. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* 58: 111-127.

Backes, A. 1999. Condicionamento climático e distribuição geográfica de *Araucaria angustifolia* (Bertol.) Kuntze no Brasil – II. *Pesquisas (Botânica)* 49: 31-52.

Backes A., Fernandes A.V. & Zeni D.J. 2000. Produção de folhedo em uma floresta com *Araucaria angustifolia* no sul do Brasil. *Pesquisas (Botânica)* 50: 97-117.

Behling, H. 2002. South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogr. Palaeoclim. Palaeoecol.* 177: 19-27.

Behling, H., Pillar, V.D., Orlóci, L. & Bauermann, S.G. 2004. Late Quaternary *Araucaria* forest, grassland (*Campos*), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogr. Palaeoclim. Palaeoecol.* 203: 277-297.

Braun-Blanquet, J. 1979. *Fitosociología: Bases para el estudio da las Comunidades Vegetales.* 3rd ed., Blume, Madrid, Spain.

Cabral, A.C., De Miguel, J.M., Rescia, A.J., Schmitz, M.F. & Pineda, F.D. 2003. Shrub encroachment in Argentinean savannas. *J. Veg. Sci.* 14: 145-152.

Connell, J.H. & Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *Am. Nat.* 111: 1119-1144.

Cook, W.M., Yao, J., Foster, B.L., Holt, R.D. & Patrick, L.B. 2005. Secondary succession in an experimentally fragmented landscape: community patterns across space and time. *Ecology* 86: 1267-1279.

Dalmagro, A.D. & Vieira, E.M. 2005. Patterns of habitat utilization of small rodents in an area of Araucaria forest in Southern Brazil. *Aust. Ecol.* 30: 353-362.

Duarte, L.S. & Dillenburg, L.R. 2000. Ecophysiological responses of *Araucaria angustifolia* (Araucariaceae) seedlings to different irradiance levels. *Aust. J. Bot.* 48: 531-537.

Duarte, L.S., Dillenburg, L.R. & Rosa, L.M.G. 2002. Assessing the role of light availability in the regeneration of *Araucaria angustifolia* (Araucariaceae). *Aust. J. Bot.* 50: 741-751.

Duarte, L.S., Dos Santos, M.M.G., Hartz, S.M. & Pillar, V.D. 2006. The role of nurse plants on Araucaria Forest expansion over grassland in south Brazil. *Aust. Ecol.* 31: 520-528.

Fargione, J., Brown, C.S. & Tilman, D. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. USA* 100: 8916-8920.

Foster, S. & Janson, C.H. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66: 773-780.

Hilton-Taylor, C. 2000. *IUCN red list of threatened species*. IUCN. Gland, UK.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton University Press, Princeton, USA.

Hueck, K. 1972. *As Florestas da América do Sul*. Ed. UnB- Ed. Polígono, São Paulo, Brazil.

Klein, R.M. 1960. O aspecto dinâmico do pinheiro brasileiro. *Sellowia* 12: 17-51.

Krebs, C.J. 2001. *Ecology: the experimental analysis of distribution and abundance*. 5th ed. Benjamin-Cummings, San Francisco, USA.

Leishman, M. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93: 294-302.

Leishman, M. & Murray, B.R. 2001. The relationship between seed size and abundance in plant communities: model predictions and observed patterns. *Oikos* 94: 151-161.

MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, USA.

Machado, R.E. 2004. *Padrões vegetacionais em capões de floresta com araucaria no planalto nordeste do Rio Grande do Sul, Brasil*. MSc. Thesis, UFRGS, Porto Alegre, Brazil.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Canc. Res.* 27: 209-220.

Moles, A. & Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* 92: 372-383.

Mueller-Dombois, D. & Ellenberg, H. 1974. *Aims and Methods of Vegetation Ecology*. John Wiley & Sons, New York, USA.

Oliveira, J.M. & Pillar, V.D. 2004. Vegetation dynamics on mosaics of *Campos* and Araucaria forest between 1974 and 1999 in Southern Brazil. *Commun. Ecol.* 5: 197-202.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. In: Likens, G.E. (ed.) *Long-Term Studies in Ecology – Approaches and Alternatives*. p. 110-135. Springer-Verlag, New York, USA. 214 p.

Pillar, V.D. 1999. The bootstrapped ordination reexamined. *J. Veg. Sci.* 10: 895-902.

Pillar, V.D. 2003. Dinâmica da expansão florestal em mosaicos de floresta e *Campos* no sul do Brasil. In: Claudino-Salles, V. (ed.) *Ecossistemas Brasileiros: Manejo e Conservação*. p. 209-216. Expressão Gráfica, Fortaleza, Brazil, 392 p.

Pillar, V.D. 2004. *MULTIV; Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling; User's Guide v. 2.3*. Departamento de Ecologia, UFRGS, Porto Alegre, Brazil (software and manual available from http://ecoqua.ecologia.ufrgs.br).

Pillar, V.D. & Orlóci, L. 1996. On randomization testing in vegetation science: multifactor comparisons of relevé groups. *J. Veg. Sci.* 7: 585-592.

Rambo, B. 1951. O elemento andino no pinhal riograndense. *An. Bot. HBR* 3: 7-39.

Rambo, B. 1956. A flora fanerogâmica dos Aparados riograndenses. *Sellowia* 7: 235-298.

Rambo, B. 1994. *A Fisionomia do Rio Grande do Sul*. 3rd ed., Ed. Unisinos, São Leopoldo, Brazil.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry.* 2nd ed., W.H. Freeman & Co., San Francisco, USA.

Tilman, D. 1996. Mechanisms of plant competition. In: Crawley, M.J. (ed.) *Plant Ecology*, 2nd ed. p 239-261. Blackwell Science, Oxford, UK.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. USA* 30: 10854-10861.

Waechter, J.L. 2002. Padrões fitogeográficos na flora atual do Rio Grande do Sul. *Ciênc. Amb.* 24: 93-108.

Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *J. Ecol.* 62: 417-428.

Plate 1. *Nurse plants and forest patches in natural grassland in São Francisco de Paula, RS, southern Brazil a) Araucaria angustifolia trees scattered in grassland. b) A small forest patch. Note the lack of a well-defined shrub layer below tree canopies. c) A large forest patch. Photographs: LS Duarte (2005).*

Table 1. Mean area of nurse trees and forest patches and sampling effort of sapling communities in forest patches at different structural development stages in natural grassland, São Francisco de Paula, RS, southern Brazil. SE = standard error.

Patch size class	Mean area (m^2) ± SE	
	Total area	Surveyed area
Nurse plants	35.9 ± 5.2	35.9 ± 5.2
Small patches	195.3 ± 37.9	15.3 ± 1.7
Large patches	1899.6 ± 255.7	209.8 ± 6.4

Table 2. Abundance of forest woody species in sapling communities at different forest development stages in natural grassland, São Francisco de Paula, RS, southern Brazil. NP = nurse plants, SP = small patches, LP = large patches. Taxonomic noise is the percent of total variance associated with non-identified species.

Species	Botanical family	Mean relative abundance (%)		
		NP	SP	LP
Araucaria angustifolia (Bertol.) Kuntze	Araucariaceae	4.17	1.14	3.85
Cabralea canjerana (Vell.) Mart.	Meliaceae	-	-	0.12
Casearia decandra Jacq.	Salicaceae	-	-	0.61
Calyptranthes grandifolia O. Berg	Myrtaceae	-	-	< 0.01
Clethra uleana Sleumer	Clethraceae	-	-	0.10
Daphnopsis fasciculata (Meisn.) Nevling	Thymelaeaceae	-	0.60	16.16
Dicksonia sellowiana Hook.	Dicksoniaceae	-	-	0.29
Drimys brasiliensis Miers	Winteraceae	1.07	2.41	9.03
Erythroxylum cuneifolium Poepp. ex O. E. Schulz	Erythroxylaceae	-	-	0.03
Eugenia uruguayensis Cambess.	Myrtaceae	-	-	0.12
Ficus luschnathiana Miq.	Moraceae	-	-	0.01
Gordonia acutifolia (Wawra) H. Keng	Theaceae	1.38	2.47	0.08
Ilex brevicuspis Reiss.	Aquifoliaceae	-	-	0.14
Ilex dumosa Reiss.	Aquifoliaceae	7.57	1.02	-

Table 2. Cont.

Ilex microdonta Reiss.	Aquifoliaceae	0.35	0.67	2.65
Ilex paraguariensis A. St-Hil.	Aquifoliaceae	-	-	0.11
Inga lentiscifolia Bent.	Fabaceae	-	-	0.01
Lamanonia ternata Vell.	Cunoniaceae	0.38	0.63	0.02
Leandra laevigata Cogn. in Mart.	Melastomataceae	-	-	0.02
Leandra sublanata Cogn. in Mart.	Melastomataceae	-	-	0.92
Matayba elaeagnoides Radlk.	Sapindaceae	-	0.16	0.11
Miconia cinerascens Miq.	Melastomataceae	-	3.93	3.17
Miconia hyemalis A. St-Hil. & Naud. ex Naud.	Melastomataceae	11.67	10.98	6.95
Miconia sellowiana Naudin	Melastomataceae	-	-	< 0.01
Mollinedia elegans Tul.	Monimiaceae	-	-	0.02
Myrsine coriacea R. Br.	Myrsinaceae	-	1.60	0.54
Myrceugenia euosma (O.Berg.) D. Legrand	Myrtaceae	0.08	-	1.26
Myrcia guianensis (Aubl.) D.C.	Myrtaceae	-	5.02	3.25
Myrcia hartwegiana (O. Berg) Kiaersk	Myrtaceae	-	-	0.23
Myrsine lorentziana Arech.	Myrsinaceae	68.14	43.81	29.17
Myrceugenia miersiana (Gardner) D. Legrand et Kausel	Myrtaceae	-	-	0.32
Myrceugenia myrcioides (Cambess.) O. Berg.	Myrtaceae	-	-	0.13
Myrcia retorta Cambess.	Myrtaceae	-	9.25	3.27
Nectandra grandiflora Nees	Lauraceae	-	-	0.01
Ocotea corymbosa Mez	Lauraceae	-	-	0.02

Table 2. Cont.

Ocotea elegans Mez	Lauraceae	-	-	0.03
Ocotea indecora Schott ex Meisn.	Lauraceae	-	-	0.01
Ocotea porosa (Mez) L. Barroso	Lauraceae	-	-	0.11
Ocotea puberula Nees	Lauraceae	-	-	0.08
Ocotea pulchella Mart.	Lauraceae	-	-	2.60
Piptocarpha axillaris Baker	Asteraceae	-	-	1.36
Piptocarpha notata Baker	Asteraceae	-	-	0.50
Podocarpus lamberti Klotzsch ex Endl.	Podocarpaceae	-	-	0.47
Psidium cattleyanum Sabine	Myrtaceae	2.01	4.03	0.42
Rollinia rugulosa Schltdl.	Annonaceae	-	-	0.42
Roupala brasiliensis Klotzsch	Proteaceae	-	0.16	0.09
Rudgea parquioides (Cham.) Müll. Arg.	Rubiaceae	-	0.11	0.21
Sapium glandulatum Pax	Euphorbiaceae	-	0.46	0.42
Siphoneugena reitzii D. Legrand	Myrtaceae	1.77	3.20	6.99
Solanum johannae Bitter	Solanaceae	-	-	0.03
Solanum pseudoquina A. St-Hil.	Solanaceae	-	-	0.04
Solanum variabile Mart.	Solanaceae	-	1.27	0.09
Tibouchina sellowiana Cogn.	Melastomataceae	-	-	0.30
Vernonia discolor (Spreng.) Less.	Asteraceae	-	3.36	2.10
Vitex megapotamica (Spreng.) Moldenke	Lamiaceae	-	-	0.46
Weinmannia paulliniifolia Pohl ex Ser.	Cunoniaceae	-	0.76	-

Table 2. Cont.

Xylosma pseudosalzmannii Sleumer	Salicaceae	-	-	0.37
Zanthoxylum rhoifolium Lam.	Rutaceae	-	-	0.03
Sub-total		98.58	97.04	99.85
Non-identified species		1.42	2.96	0.15
Total		100.00	100.00	100.00
Taxonomic noise		0.82	0.12	0.02

Table 3. Species distribution in sapling communities in forest patches, at different structural development stages, in natural grassland, São Francisco de Paula, RS, southern Brazil. N_T: Total species number; N_E: Exclusive species number. Percent values in parentheses refer to the proportion of exclusive species in the total number of species.

Site	N_T	Exclusive species		
		N_E	%	
			Residents	Colonizers
Nurse plants	9	0	0	0
Small patches	23	1 (4%)	0	4
Large patches	56	33 (59%)	18	82

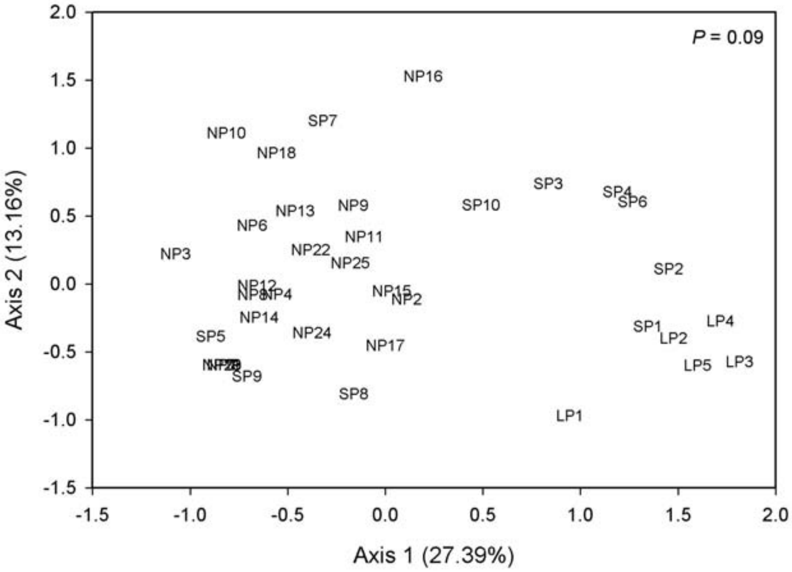

Fig. 1. *PCoA ordination of sapling communities in forest patches at different structural development stages, in natural grassland, São Francisco de Paula, southern Brazil. NP = nurse plants, SP = small patches, LP = large patches.* P *value for axis 1 generated by bootstrap resampling.*

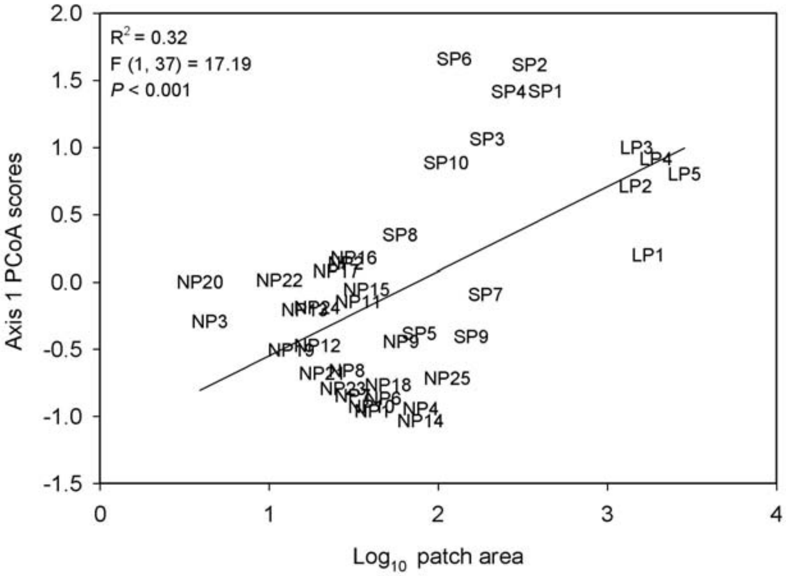

Fig. 2. *Association between the first PCoA ordination axis and patch size in natural grassland, São Francisco de Paula, RS, southern Brazil. NP = nurse plants, SP = small patches, LP = large patches.*

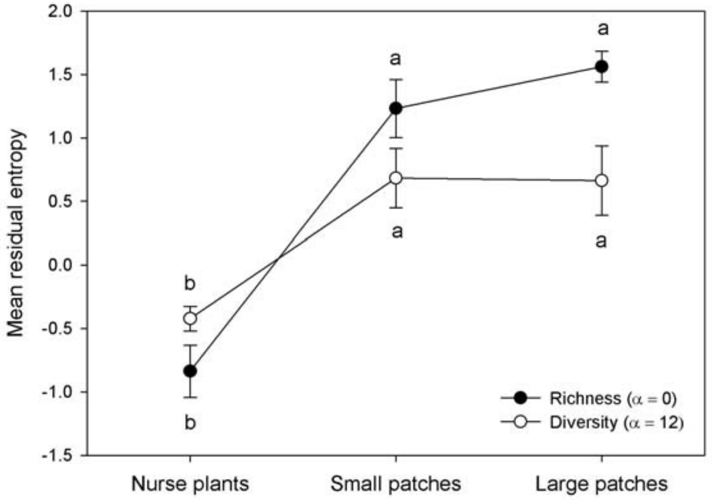

Fig. 3. *Richness and diversity patterns in three forest patches, at different structural development stages, in natural grassland, São Francisco de Paula, RS, southern Brazil. Mean values calculated on residuals of a regression of richness or diversity on sampling effort. Lines crossing mean values are standard errors. Mean richness/diversity values followed by the same letter do not differ significantly between patch size classes (*$\alpha = 0.05$*).*

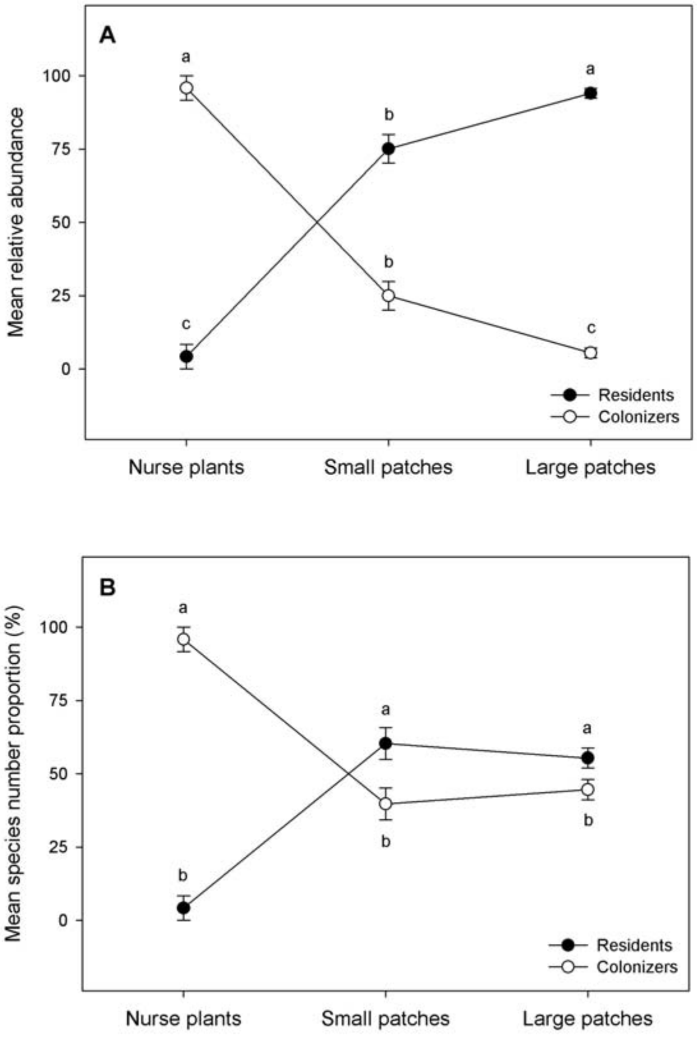

Fig 4. *Recruitment patterns of resident and colonizer species at different forest development stages in natural grassland, São Francisco de Paula, RS, southern Brazil. A) Mean relative abundance and B) species number proportion. Values are means and lines crossing mean values are standard errors. Mean values followed by different letters differ significantly between patch size classes (*$\alpha = 0.05$*).*

Capítulo 4. Plant dispersal strategies and the colonization of *Araucaria* forest patches in a grassland-forest mosaic[3]

Duarte, Leandro da S.[1*]; Carlucci, Marcos B.[1,2]; Hartz, Sandra M.[1,3] & Pillar, Valério D.[1,4]

[1]*Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, CP 15007, Porto Alegre, RS 91501-970, Brazil;*

[2]*E-mail: mbcarlucci@ecologia.ufrgs.br,* [3]*E-mail: sandra.hartz@ufrgs.br,* [4]*E-mail: vpillar@ufrgs.br;*

[*]*Corresponding author*; *Fax +55 5133167626; E-mail leandro.duarte@ufrgs.br; duarte.ldas@gmail.com*

Resumo

Questões: Em um mosaico floresta-campo natural, qual a influência da filogenia e atributos de diásporos relacionados à atração de dispersores (DAT) sobre (1) o *trade-off* tamanho de semente/número de sementes (SSNT) em espécies lenhosas colonizando manchas florestais, e (2) sobre a freqüência das espécies? (3) Qual a influência da área da mancha florestal sobre o tamanho e o número médio das sementes em nível de comunidade, e (4) até que ponto a filogenia e DAT expressos em nível de espécie afetam esta associação?

---

[3] Manuscrito aceito para publicação no periódico *Journal of Vegetation Science* em 12 de abril de 2007.

Local: Um mosaico de campo e floresta com *Araucaria* em São Francisco de Paula, Rio Grande do Sul, Brasil (29°28'S e 50°13'W).

Métodos: Manchas florestais de diferentes tamanhos num sítio campestre recuperando-se há 10 anos de distúrbios antrópicos foram amostradas através da abundância relativa de plantas lenhosas jovens dispersas por vertebrados. Nós descrevemos as espécies colonizadoras de acordo com as relações filogenéticas e DAT (tipo, tamanho e cor do diásporo). Usando um método de partição de variação nós analisamos suas influências sobre SSNT e sobre a freqüência das espécies nas manchas. Em n´vel de comunidade nós ajustamos um regressão do tamanho e número médios de sementes em funçaõ da área da mancha florestal, e usando resíduos avaliamos como estas realções foram afetadas pela filogenia e DAT expressos em nível de espécie.

Resultados: 1) Filogenia e DAT explicaram a maior parte da variação no tamnaho das sementes e no número de sementes por diásporo e (2) controlando a influência da filogenia e do DAT nós descobrimos que a feqüência das espécies nas manchas florestais foi positivamente associada com o número de sementes em seus diásporos, e negativamente associada com o tamanho de suas sementes. 3) O tamanho e o número médio de sementes em nível de comunidade foram positivamente associados com a área da mancha, e quando as influências de filogenia e DAT sobre o tamanho das sementes em nível de espécie foram removidas, (4) esta relação tornou-se mis forte para tamanho de semente e mais fraca para número de sementes.

Conclusões: 1) Alocação de energia para dispersão em detrimento de sobrevivênvcia da prole aumentou o sucesso no estabelecimento de espécies colonizadoras em manchas florestais, apesar da variação em seus diásporos atribuída a relações filogenéticas e DAT. 2) Embora a área da mancha exerça uma pressão seletiva sobre o tamanho das sementes, possivelmente preferências de habitat de dispersores também influencie a colonização das manchas.

Palavras-chave: Floresta com *Araucaria*, Campos, Nucleação, *Trade-off* tamanho/número de sementes, SSNT.

Abstract

Questions: In a natural grassland-forest mosaic, (1) what is the influence of phylogeny and diaspore traits related to disperser attraction (DAT) on seed size/number trade-off (SSNT) in woody species colonizing forest patches, and (2) on the frequency of the species? (3) What is the influence of forest patch area on mean seed size and number at the community level, and (4) to what extent phylogeny and DAT expressed at the species level affect this relationship?

Location: A mosaic of *Campos* grassland and *Araucaria* forest in São Francisco de Paula, Rio Grande do Sul, Brazil, at about 29°28'S and 50°13'W.

Methods: Forest patches of different sizes in a grassland site recovering for 10 years from human disturbances were surveyed by the relative abundance of vertebrate-dispersed woody saplings. We described colonizer species according to taxonomic phylogenetic relationships and DAT (diaspore type, size and color). By using a variation partitioning method we analyzed their influence on SSNT and on frequency of species in the patches. At the community level we regressed mean seed size and number on forest patch area, and by using residuals evaluated how these relationships were affected by phylogeny and DAT expressed at the species level.

Results: 1) Phylogeny and DAT mostly explained seed size and seed number per diaspore variation and (2) by controlling phylogeny and DAT influence we found that the frequency of species in forest patches was positively associated with their seed number in the diaspores, and negatively associated with their seed size. 3) Mean seed size and seed number at the community level were positively associated with patch area, and when phylogeny and DAT influences on seed size at the species level were removed (4) this relationship was stronger for seed size and weaker for seed number.

Conclusions: 1) Energy allocation to dispersal in detriment of offspring survival increased the successful establishment of colonizer species in forest patches, despite of phylogenetic relationships and DAT variation in their diaspores. 2) Although patch area exerted a selective pressure on seed size, possibly habitat preferences of the dispersers also influenced patch colonization.

Keywords: *Araucaria* forest, *Campos* grassland, nucleation, seed size number trade-off, SSNT.

Abbreviations: DAT = Diaspore traits related to disperser attraction, PCA = Principal Components Analysis, SNT = Stochastic Niche Theory, SSNT = Seed size/number trade-off; UNTBB = Unified Neutral Theory of Biodiversity and Biogeography.

Nomenclature: APG (2003); Anon. (2005)

Introduction

The balance between the recruitment capacity of resident species and the survivorship of immigrant species through dispersal events drives community dynamics in most habitats. For the last 40 years, dispersal-based neutral models were the guiding paradigms concerning the structure and dynamics of insular landscapes. The Equilibrium Theory (MacArthur & Wilson 1967) explained species richness from colonization and extinction events across habitat gradients in area and isolation. More recently, the Unified Neutral Theory of Biodiversity and Biogeography (UNTBB) formulated by Hubbell (2001) suggested that community diversity components (richness and relative abundance) could be explained by the zero-sum dynamics, assuming that all species are functionally equivalent in exploiting the environment (see also Hubbell 2005). Further, the maximum number of individuals (J) supported by the habitat (a function of habitat area), the probability of immigration of new species into it (m), and the speciation rate (v) should determine the species richness and community structure.

The expansion of woody vegetation over natural grasslands is a worldwide phenomenon (Scholes & Archer 1997; Bond & Midgley 2000; Bond et al. 2003). Yet, most theoretical framework concerning the structure and dynamics of forest patches has been focused on the fragmentation of continuous habitats deforested by human activities (e.g. Schelhas & Greenberg 1996). The establishment of pioneer trees and shrubs in grassland modifies the resource availability and environmental conditions beneath its crowns, and creates suitable habitats for the establishment of forest species (e.g. Callaway 1995; Bruno et al. 2003). Since those pioneer species constitutes the establishment nuclei for the development of forest patches, Yarranton & Morrison (1974) named this process *nucleation*. At its initial phase, the nucleation of forest patches into grassland relies on the successful dispersal of plant diaspores (e.g. seeds and fruits) from a source community, and on the capacity of the colonizer in exploiting the resources in the new habitat. Following UNTBB, the probability m_i of the colonizer species i establishing into a forest patch is determined by the abundance of i in the source area times its reproductive effort, defined as the allocation rate of energy to reproduction (Begon et al. 1995). These two components determine the propagule pressure exerted by the species i on the sink patches (e.g. Lockwood et al. 2005; Colautti et al. 2006), that is, the abundance of diaspores produced by a plant population times the frequency of diaspore production events. However, as forest patch nucleation proceeds, shrubs and trees gradually achieve the reproductive phase and produce a resident sapling community, which progressively occupy most habitat space (Yarranton & Morrison 1974; Fargione et al. 2003; Cook et al. 2005), precluding the arrival of new colonizers (m decreases). Thus, nucleation dynamics involves an initial phase determined by external input of colonizer plants from the source area (high m probability), and a subsequent development phase, where local offspring recruitment by mature trees drives vegetation dynamics (low m probability). At this latter phase, m_i does not depend only on the dispersal patterns of the source community, but also on the resistance of the patch community to the immigration of new species. In such scenario, the probability of a colonizer to survive until maturity depends on its capacity to explore the resources left available by the resident species, as proposed by the Stochastic Niche Theory (SNT, Tilman 2004).

Adaptive traits related to colonization of new habitats can increase the probability of a colonizer species successfully establish in forest patches (see Westoby et al. 2002; Coomes & Grubb 2003). In nucleation process, colonization strategies involve the efficient dispersal and the high survival capacity of the colonizer offspring in the new habitat. Since environmental resources necessary to reproduction are limited (see Venable 1996), plants experience a trade-off involving the allocation of energy to dispersal (higher seed number) or offspring survival (higher seed size), the so-called seed size/number trade-off (SSNT) (e.g. Turnbull et al. 1999; Leishman 2001). To optimize dispersal, plants should produce the highest possible number of seeds per individual parent (Ehrlén & Eriksson 2000). On the other hand, the survival capacity of new individuals is improved if more reserves are allocated to seeds (Harper et al. 1970; Westoby et al. 1990; Kidson & Westoby 2000; Coomes & Grubb 2003; Moles et al. 2005; Moles & Westoby 2006). The product of the fitness function of the seed size in a given habitat times the number of seeds per diaspore defines the fitness of the parent-plant (Venable 1996).

SSNT is closely associated with colonization strategies across a variety of habitats (Foster & Janson 1985; Leishman 2001; Jakobsson & Eriksson 2000; Moles & Westoby 2004). However, its functional significance has been questioned, since other relevant factors, like dispersal agents and phylogeny are correlated with seed traits (Westoby et al. 1990; Kelly & Purvis 1993; Kelly 1995), and the correspondence between seed size and habitat type might be due to correlated factors other than the differential survivorship capacity of species with distinct seed sizes (see Leishman & Murray 2001).

Araucaria forest is an ecosystem widespread in southern Brazilian highlands. These forests often form mosaics with *Campos*, which is a natural type of grassland (Rambo 1994). *Araucaria* forest expansion over grassland in southern Brazil was already demonstrated by paleopollen evidence (Behling 2002; Behling et al. 2004), either gradually by edge dynamics (Oliveira & Pillar 2004), or by nucleation of forest patches in the grassland (Klein 1960; Duarte et al. 2006a). In a recent study, we found that in *Araucaria* forest patches released for ten years from burning and cattle grazing disturbances the recruitment of woody saplings was strongly associated with patch area (Duarte et al. 2006b). Isolated *Araucaria angustifolia* individuals scattered in the grassland act as nurse plants, promoting the establishment of colonizer forest species (see also Duarte et al. 2006a). In small patches, consisting of few adult trees (capable to recruit resident saplings) plus a variable amount of woody saplings mixed to a remnant grass layer and lacking a clear vertical structure, approximately 30% of woody saplings were colonizers, while in more developed large patches, with a structured tree layer, a well-defined shrub layer, and a herb layer consisting exclusively of forest species, colonizer plants occupied only 6% of the relative abundance of saplings (Duarte et al. 2006b). Taking m as the probability of a dead sapling to be replaced by a new colonizer, the proportion of colonizers in the community might estimate m for that community. Therefore, habitats beneath nurse plants, small patches and large patches could be addressed as showing, respectively, high, intermediary and low m probabilities (Fig. 1).

Our objective in this study was to analyze the role of SSNT in the colonization of *Araucaria* forest patches by forest woody species. We analyzed the phylogenetic component of SSNT variation in colonizer plants, and evaluated the influence of diaspore traits related to disperser attraction (DAT) on SSNT (see Westoby et al. 1990). For this, we restricted our analyses to vertebrate-dispersed species, which represented the vast majority (96% of the total abundance) of woody plants colonizing *Araucaria* forest (Duarte et al., unpubl.). We verified if the frequency of occurrence of forest woody species in *Araucaria* forest patches was explained by SSNT itself, or rather by indirect effects of phylogeny and DAT on SSNT. Furthermore, we analyzed the effect of SSNT on the colonization of forest patches of different sizes and m probabilities. Also in this case, we tested the effect of phylogeny and DAT on SSNT.

Material and Methods

Study area

The study was conducted at the Pró-Mata Research and Nature Conservation Center (CPCN Pró-Mata), situated at about 29°28'S and 50°13'W, at ca. 900 m a.s.l.. The Center has a 4500 ha area, in São Francisco de Paula, Rio Grande do Sul State, southern Brazil. The study site was comprised of ca. 78 ha *Campos* grassland surrounded by continuous *Araucaria* forest. Since 1994 cattle grazing and burning practices were terminated throughout the area, allowing increasing regeneration in forest patches scattered in the grassland (Duarte et al. 2006b), and more biomass accumulation and woody plant establishment in the open field (Oliveira and Pillar 2004). The regional climate is classified according to Köppen's system as Cfb (Moreno 1961), which is characterized by subtropical (C), rainy, with precipitation uniformly distributed through the year (f), and presenting warm summers (b). The annual mean temperature is ca. 14.5°C, with freezing temperatures occurring from April to November (Backes 1999), and the annual mean rainfall is 2252 mm equally distributed throughout the year (Backes et al. 2000). The presence of species phytogeographically related to Austral-Antarctic and Andean floras distinguish *Araucaria* forest communities from more tropical facies of Brazilian Atlantic forests (Rambo 1951). The most physiognomically important tree species is *Araucaria angustifolia*. Some other typical species found in those forests are *Podocarpus lamberti*, *Drimys brasiliensis*, *Dicksonia sellowiana*, and several species of Myrtaceae, Melastomataceae and Lauraceae.

Sampling methods

We analyzed woody sapling communities in 37 forest patches from April 2003 to February 2005 (Duarte et al. 2006b). Forest patches were described by the abundance of vertebrate-dispersed colonizer and resident species. Colonizer species were those occurring in the same patch size class only as saplings (individuals < 5 cm of diameter at breast height) and resident species were those occurring as sapling and as assumed mature plants in the same patch size class (individuals > 5 cm of diameter at breast height). We choose classifying species into residents and colonizers based on their occurrence in each patch size class instead of each patch individually, to control spatial mass effects within the distinct patch size classes (Kunin 1998). Thus, if a species was resident (adults plus saplings) in a given large patch, but occurred in another large patch only as saplings, we considered it resident for all large patches, since its occurrence exclusively as saplings did not allow us defining whether it was dispersed from the source area or from another large patch.

Forest patches were divided into three size classes: The smallest sampling units were 23 *Araucaria angustifolia* nurse plants isolated in the grassland. We considered 'isolated' any tree lacking a neighbor woody plant touching its crown. In this case, crown cover was taken as the patch size and was estimated from crown projection diameter (mean crown area ± standard error = 35 m^2 ± 5.2). All woody saplings occurring beneath the tree canopy were identified. We also sampled nine small forest patches, defining a patch as any group of forest woody plants with at least one adult tree and accompanying shrubs, forming a continuous canopy, surrounded by a continuous herb layer (Cabral et al. 2003). The small patches lacked a clear vertical structure, and in general had few adult trees, mostly of *Myrcia retorta*, *Araucaria angustifolia*, *Myrcia guianensis* and *Myrsine lorentziana*, plus a variable amount of woody saplings (Duarte et al. 2006b). The canopies were considerably open, allowing grassland species to resist to some extent to forest development. We estimated the total patch area as an ellipse, using the maximum length and maximum width of the patch canopy (mean patch area ± standard error = 195.3 m^2 ± 37.9). All woody individuals with diameter at breast height > 5 cm were sampled. Along the major diameter axis of each patch we delimited 1.7 m x 1.7 m quadrats, within which all forest species saplings were identified. We surveyed on average five quadrats per sampling unit, which represented 8% of the total area of the small patches. Furthermore, we analyzed data from five large patches, which presented high structural development compared to nurse plants and small patches (mean patch area ± standard error = 1899.6 m^2 ± 255.7*)*. They had a structured tree layer, formed mainly by *Myrcia guianensis, Drimys brasiliensis, Myrcia retorta* and *Araucaria angustifolia,* a well-defined shrub layer, and a herb layer consisting exclusively of forest species. Data on large patches were provided by Machado (2004). The author used 5 m x 5 m quadrats to sample adult individuals. On average, 16 quadrats were surveyed per sampling unit, which accounted for 45% of the total area of the large patches. Saplings of woody species were sampled in 1.7 m x 1.7 m quadrats delimited within the larger quadrats. On average, 72 quadrats were surveyed per sampling unit, which accounted for 11% of the total area of the large patches. From the data we extracted a community matrix **C** describing the relative abundances (proportions) of *p* vertebrate-dispersed colonizer species only (rows) in *n* patches (columns).

Phylogeny

We described taxonomically each colonizer species according to the phylogenetic classification of Angiosperms proposed by APG II (APG 2003). For this, we built a binary matrix **F**, defined by *t* taxonomic clades (rows), from higher monophyletic groups (like Magnoliids and Core Eudicots), to orders, families and genera, and *p* colonizer species (columns). We used matrix **F** to evaluate the phylogenetic determinants of SSNT.

Diaspore traits

Information on plant diaspores was obtained from a vast literature review and field and herbarium observations (see Appendix 1). Vertebrate-dispersed species colonizing the patches (from matrix **C**) were described by seed size and number. We evaluated seed size as a quantitative continuous variable (mean seed diameter in mm), and seed number per diaspore as quantitative discrete variable categorized in three classes (1- single seeded diaspore, 2- two to five seeds per diaspore, 3- more than five seeds per diaspore). The data defined the matrix $\mathbf{D}_1$, describing q_1 diaspore traits (the variables seed size and number, in rows) in p colonizer species (columns).

Colonizer species were also described by diaspore type, size and color, which are traits related to disperser attraction (DAT) (Ridley 1930; Howe & Smallwood 1982; Van der Pijl 1982; Gauthier-Hion et al. 1985; Wheelwright 1985). Diaspores were categorized into four types: berries, drupes, arillate seeds and others (figs, pods or compound fruits). Also, diaspores were categorized into three size classes (small, medium and large). For this, we calculated the mean diaspore diameter (in mm) ± 95% confidence interval ($\bar{\phi} \pm \mathrm{CI}_{95\%}$) for the colonizer species pool. Diaspores with mean diameter below $\bar{\phi} - \mathrm{CI}_{95\%}$ and above $\bar{\phi} + \mathrm{CI}_{95\%}$ were classified, respectively, as small and large diaspores, while those with diameter values within the $\bar{\phi} \pm \mathrm{CI}_{95\%}$ interval were classified as medium-sized. The variables diaspore type and size so defined were expanded into seven binary (dummy) variables. As well, each diaspore color defined a binary variable, and in this case a diaspore presenting more than one color was recorded accordingly for all variables. The data defined a matrix $\mathbf{D}_2$ describing q_2 diaspore traits (DAT, rows) in p colonizer species (columns).

Data analyses at the species level

We addressed the influence of phylogeny, DAT, phylogenetically structured DAT and the unexplained variation on seed size and number using the variation partitioning method proposed by Desdevises et al. (2003). The method is based on the decomposition of the total variation (R^2) of the dependent variable explained by two sets of independent variables (in this case, phylogeny and DAT) into four components: a is the fraction of the variation explained by phylogeny, b is the fraction of the variation explained by phylogenetically structured DAT, c is the fraction of the variation explained by DAT, and d is the residual variation.

For this we performed Principal Components Analyses (PCA) (Legendre & Legendre 1998) on matrices **F** and $\mathbf{D}_2$ (containing only DAT variables), using Pearson correlation as similarity index. This was followed by forward stepwise multiple linear regressions using as dependent variables seed size and seed number (taken from matrix $\mathbf{D}_1$), and as independent variables the PCA ordination axes obtained from matrix **F** in one set of regressions (fraction a+b) and from $\mathbf{D}_2$ in another set of regressions (fraction b+c). Using PCA scores rather than trait values themselves prevented the multicollinearity in the regression analyses (Sokal & Rohlf 1981). Then, we performed a multiple regression analysis with the same dependent variables and with the significant PCA axes of the preceding stepwise regressions (from both **F** and $\mathbf{D}_2$) as the independent variables (fraction a+b+c). The variation components were then obtained by subtraction:

$$
\begin{aligned}
a &= R^2(a+b+c) - R^2(a+c) \\
b &= R^2(a+b) + R^2(b+c) - R^2(a+b+c) \\
c &= R^2(a+b+c) - R^2(a+b) \\
d &= 1 - R^2(a) - R^2(b) - R^2(c)
\end{aligned}
$$

We removed the non-significant ordination axes from regression due to the high multicollinearity generated by their presence in the last regression, which would inflate the R^2 of the component *b*.

We evaluated the correlation between seed size and number (from matrix $\mathbf{D}_1$) and tested the significance using randomization testing (Pillar 2006). The correlation was then re-evaluated using the residuals of the abovementioned regressions of seed size and number on **F** and $\mathbf{D}_2$, to assure that SSNT patterns were free from any influence of phylogenetic relationships and DAT (see Kelly 1995).

We also used regression residuals to evaluate the effect of seed size and seed number on the frequency of the species in the patches. The frequency of a given species was obtained from matrix **C** and expressed as the proportion of patches occupied by the species. For this, we performed a multiple regression analysis of seed size and number residuals (independent variables) on the species frequency transformed by log (x+1) (dependent variable). All variables were centralized and standardized by the standard deviation.

Data analyses at the community level

By matrix multiplication, $\mathbf{R}_1 = \mathbf{D}_1\mathbf{C}$, where matrix $\mathbf{R}_1$ described *n* forest patches (columns) by seed size and number (rows). Since species quantities were relative abundances values ranging from 0 to 1 (Duarte et al. 2006b), $\mathbf{R}_1$ recorded mean seed size and number values of the colonizer species in each forest patch.

We evaluated the variation in mean seed size and seed number (matrix $\mathbf{R}_1$) of colonizer plants in forest patches of different sizes through linear regression analyses. Since the matrix $\mathbf{R}_1$ (derived from $\mathbf{D}_1$) possibly contained components of variation explained by phylogeny, DAT and phylogenetically structured DAT, we also evaluated the variation of mean seed size and seed number as predicted by these variables. For this, we multiplied the predicted values of the regressions of $\mathbf{D}_1$ on **F** and $\mathbf{D}_2$ (fraction *a*+*b*+*c* in the previous analyses at species level) by the community matrix **C**, obtaining the matrix $\mathbf{R}_1(\mathbf{F},\mathbf{D}_2)$, which described patches by the mean seed size and number as predicted by phylogeny, DAT and phylogenetically structured DAT. The variables in $\mathbf{R}_1(\mathbf{F},\mathbf{D}_2)$ were submitted to linear regression analyses using patch area as independent variable. Further, we analyzed the effect of patch area on seed size and number by controlling the effects of phylogeny, DAT and phylogenetically structured DAT. For this we multiplied the residuals of the abovementioned regressions of $\mathbf{D}_1$ on **F** and $\mathbf{D}_2$ by the community matrix **C**, obtaining matrix $\mathbf{R}_1(\varepsilon)$, which described patches by the variation of mean seed size and number that were not explained by phylogeny, DAT and phylogenetically structured DAT. The variables in matrix $\mathbf{R}_1(\varepsilon)$ were submitted to linear regression analyses using patch area as independent variable. All variables were centralized and standardized by the standard deviation.

Regression analyses were carried using the software SigmaStat v. 3.11 (Anon. 2004) and STATISTICA 6 (Anon. 2001). All other analyses were performed using the MULTIV 2.4 (Pillar 2006) statistical software.

Results

The vast majority of the 38 vertebrate-dispersed colonizer plants presented bright-colored, small fleshy diaspores. Berries and drupes represented 84% of diaspores, while the remaining 16% were arillate seeds (8%), compound fruits, figs and pods (others, 8%) (Fig. 2a). Most diaspores (ca. 68%) presented diameters smaller than ten millimeters, while only 5% had diaspores larger than 35 millimeters (Fig. 2b). Also, diaspores were predominantly black, red or violet (Fig. 2c). Seed diameter smaller than four millimeters predominated in colonizer plants

(55% of total species number), while only 5% of species showed seed diameter larger than 12 mm (Fig 2d). Colonizer species with single-seeded diaspores comprised 39% of total species number, while species with few seeds (between two and five) and with many seeds (more than five) accounted for 37% and 24% of total species number, respectively (Fig. 2e).

The ordination of vertebrate-dispersed colonizer species according to DAT variables (matrix $\mathbf{D}_2$) indicated major groups of variables associated with disperser attraction (Fig. 3). Along the first PCA axis, which represented 19% of total variation in the data, two main groups of variables were observed. While large compound fruits, figs or pods, yellow, brown or green-colored were positively correlated with the first ordination axis ($P \leq 0.05$), small berries or drupes, black, red or violet-colored were negatively correlated with the same axis ($P \leq 0.01$). These two major groups of DAT variables were negatively correlated with the second PCA axis, which represented 15% of the total variation in the data ($\mathrm{P} \leq 0.07$). A third group, formed by medium-sized arillate seeds, orange or white-colored, was positively correlated with the second ordination axis ($P \leq 0.02$).

Phylogeny, DAT and phylogenetically structured DAT mostly determined the variation in seed size and seed number per diaspore in colonizer species (Fig. 4). However, phylogeny and DAT had low effect on the frequency of occurrence of colonizer species in patches (Fig. 4). The negative correlation between seed size and seed number per diaspore was also determined by phylogeny and DAT (Fig. 5a); after removing the effects of phylogeny and DAT from seed size and seed number the correlation between these traits disappeared (Fig. 5b). Also, using the same residuals, the frequency of occurrence of colonizer species in patches was positively associated with the number of seeds present in the colonizer plant diaspores, and negatively associated with the size of the colonizer plant seed (Table 1).

Both mean seed size (Fig.6a) and mean seed number (Fig.6b) variation of colonizer species at community level were significantly explained by patch area; in both cases, the relationship among the dependent variables (seed size or seed number) and the independent variable (patch area) was positive. The seed size variation fraction predicted by phylogeny, DAT and phylogenetically structured DAT (Fig. 6c) was not significantly explained by patch area variation; on the contrary, those factors significantly explained the variation of mean seed number in patches of different sizes (Fig. 6d). When phylogeny, DAT and phylogenetically structured DAT effects were removed from the variation of seed size and number at the species level, patch area had a significant effect, at the community level, on mean seed size (Fig. 6e), but not on mean seed number (Fig. 6f).

Discussion

The UNTBB (Hubbell 2001) predicts that the probability of immigration *m* of a given species into a habitat patch (so-called local community) depends only on the community structure of the source area (so-called meta-community), given that the habitat space is fully occupied (achieved *J*). Following this prediction, we expected that the frequency of occurrence of colonizer species in *Araucaria* forest patches would not be related to dispersal trade-offs. Indeed, we found that at the species level the association between seed size and seed number in species colonizing *Araucaria* forest patches was mostly explained by phylogenetic relationships between species and by diaspore attributes related to disperser attraction (DAT) (see Westoby et al. 1990; Kelly & Purvis 1993; Kelly 1995). However, we also observed that phylogeny and DAT explained only a small fraction of the variation of colonizer species frequency in forest patches. Furthermore, after removing their influence on seed size and seed number, we observed that species frequency was significantly explained by SSNT: colonizer species with many small seeds were more frequent that those with few large seeds. In other words, the colonization of forest patches was more dependent on the seed abundance (investment in dispersal) than on the reserve content of the seed (investment in survival), in opposition to the predicted neutrality of plant colonization assumed by UNTBB.

From a theoretical perspective, our findings suggest that, given a colonizer species i, and assuming that all patches achieved J, and that m is constant, energy allocation to dispersal (higher seed number) in detriment of offspring survival (higher seed size) increases the probability (m_i) of successful establishment into a new habitat. If we incorporate this niche component of fitness to higher-order determinants of dispersal success, like the propagule pressure of the species i on the patches and its abundance in the source community (see Venable 1996), we could generate detailed population-based models of nucleation of forest patches on open areas. Future studies must investigate the effects of the community structure in the source areas (in this case the continuous *Araucaria* forest) and the fruiting phenology on the abundance patterns of the colonizer species in forest patches, in order to depict a more complete portrait of the mechanisms underlying the nucleation of forest patches in natural grassland ecosystems.

Further, smaller seeds might be less susceptible to predation than larger seeds (Leishman 2001, Moles et al. 2003), and this predation avoidance might counterbalance the advantage of more seed reserves in large-seeded species. In a recent study, we observed that the removal of *Araucaria angustifolia* large seeds (mean diameter ≅ 36 mm) by small mammals was more intense in forest patches than in the surrounding continuous forest (Brum et al., unpubl.). Small mammals in our study site comprise mostly rodents (Pedó 2005), which are important seed predators in the Neotropics (e.g. Vieira et al. 2003). However, Mack (1998) suggested that large seeds might be more resistant to seed predators than small seeds, since the chance of the former´s embryo surviving after the removal of the reserve tissue is higher than that of the latter. The interaction between seed size and seed predation is still controversial, and deserves further attention.

According to the Stochastic Niche Theory (SNT) proposed by Tilman (2004), the probability of a species colonizing a forest patch survive until maturity depends on its capacity to explore the resources left available by the resident species. As a forest patch develops and plants achieve the reproductive phase, the habitat area is progressively occupied by resident species, decreasing the probability of immigration (Fargione et al. 2003, Cook et al. 2005); therefore, traits enabling plant survival might favor plant colonization. The evidence that plant species with large seeds are superior competitors in the initial establishment of seedlings has solid theoretical an empirical basis (Leishman et al. 2000; Dalling & Hubbell 2002; Westoby et al. 2002; Moles & Westoby 2004; Moles et al. 2005; Moles & Westoby 2006). Leishman et al. (2000) pointed out the consistent positive association between seed size and shading tolerance (see also Foster & Janson 1985). Adult individuals of large-seeded species might also have greater canopy area and longevity than those of small-seeded species (Moles & Westoby 2004; Moles et al. 2005; Moles & Westoby 2006). On the other hand, many small-seeded species are considered better colonizers than large-seeded species. Leishman (2001) found a positive relationship between the number of seeds in the seed rain and species abundance in a calcareous grassland community.

Following SNT, colonizer plants with large seeds might have a higher probability of successful establishment than small-seeded species (see also Cook et al. 2005). In our study, we observed a positive association between seed size and patch area. Furthermore, seed number of colonizer species was also positively associated with patch area. Therefore, as *m* varied as a function of patch occupancy by resident species, a shift in the attributes of the colonizer plants arriving in patches was observed. While seed size was directly affected by patch area, seed number was determined mostly by phylogeny and DAT effects. Our results suggest that large-seeded colonizers present an advantage over small-seeded species in colonizing larger patches. However, the strongest association between seed size and patch area emerged only when we removed the effects of phylogeny and DAT. It suggests that the association between seed size and plant survivorship were complex, and might be influenced in a variable extent by other components involved in the diaspore dispersal to new colonization sites (see Leishman & Murray 2001). In this study, we focused only on vertebrate-dispersed species, whose dispersal is recognizably influenced by the habitat preferences (Nathan & Muller-Landau 2000), as well as by morphological attributes of dispersers. Wheelwright (1985) found a relationship between diaspore sizes and gape width of disperser birds. Jordano (1995) also observed that diaspore diameter was related to dispersal syndromes, even after the removal of phylogenetic effects. Further, Westoby et al. (1990) and Kelly (1995) found a significant association between seed size and dispersal agents. Kelly (1995) observed that heavier seeds tended to be preferentially dispersed by mammals than lighter seeds. Since most colonizer plants in *Araucaria* forest patches are dispersed by vertebrates (Duarte et al., unpubl.), understanding how biological and ecological attributes of dispersers influence the dispersal of colonizer plant diaspores in patches is crucial to the understanding of nucleation dynamics.

Although the theoretical framework provided by neutral (UNTBB, Hubbell 2001) and niche models (SNT, Tilman 2004) represent excellent starting points for the development of general nucleation models, they do not include higher hierarchical mechanisms, like plant-animal interactions, which are essential for nucleation dynamics. In our study we observed that even major trade-offs related to plant dispersal success (like SSNT) can be influenced by co-adaptative systems, in this case represented by diaspore traits related to disperser attraction. Furthermore, studies focusing on the nucleation dynamics of *Araucaria* forest patches over *Campos* grassland are fundamental tools for the development of conservation strategies concerning this very threatened (and poorly known) ecosystem. Surprisingly, in some studies performed in natural *Araucaria* forest-*Campos* grassland edges (e.g. Baldissera & Ganade 2005; Fontoura et al. 2006), a misleading interpretation of ecological dynamics (fragmentation instead of nucleation) has prevailed. Although habitat fragmentation and nucleation share some fundamental properties, such as species-area relationship and edge effects, they consist in totally different processes. Fragmentation is commonly associated with ecosystem disturbances, particularly man-made ones, and involves habitat and diversity losses, since a considerable part of species exposed to forest fragmentation are functionally related to forest interiors. Nucleation of forest patches over natural grasslands, in opposition, is a natural dynamic process involving different community types merged in a mosaic landscape, and involves the enhancement of biological diversity. We hope that the development of nucleation-based ecological theories may clarify the differences between these processes, providing a better understanding for appropriate conservation and management of these complex landscapes.

Acknowledgements

The authors thank botanists Dr. Maria Leonor D’El Rei Souza (UFSC) and Manuela Boleman Wiesbauer, who kindly provided information about some plant diaspores, Rafael E. Machado for kindly providing us the data on the presence of species in large forest patches. We also thank David Ackerly and Alicia Acosta for valuable suggestions on the manuscript. This study had logistic support from CPCN Pró-Mata PUCRS and was funded by research grants and fellowships from CAPES (project 005/02) and CNPq (project 141810/2003-3).

References

Anon. 2001. *STATISTICA (data analysis software system)*, version 6. www.statsoft.com.

Anon. 2004. *SigmaStat for Windows* v. 3.11. Richmond, USA.

Anon. 2005. *IPNI - The International Plant Names Index*. URL: http://www.ipni.org [accessed from March to August 2005].

APG 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399-436.

Backes, A. 1999. Condicionamento climático e distribuição geográfica de *Araucaria angustifolia* (Bertol.) Kuntze no Brasil – II. *Pesquisas (Botânica)* 49: 31-52.

Backes A., Fernandes A.V. & Zeni D.J. 2000. Produção de folhedo em uma floresta com *Araucaria angustifolia* no sul do Brasil. *Pesquisas (Botânica)* 50: 97-117.

Baldissera, R. & Ganade, G. 2005. Predação de sementes ao longo de uma borda de Floresta Ombrófila Mista e pastagem. *Acta Bot. Bras.* 19: 161-165.

Behling, H. 2002. South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeogr. Palaeoclim. Palaeoecol.* 177: 19-27.

Behling, H., Pillar, V.D., Orlóci, L. & Bauermann, S.G. 2004. Late Quaternary *Araucaria* forest, grassland (*Campos*), fire and climate dynamics, studied by high-resolution pollen, charcoal and multivariate analysis of the Cambará do Sul core in southern Brazil. *Palaeogeogr, Palaeoclim., Palaeoecol* 203: 277-297.

Begon, M. Harper, J.L & Townsend, C.R 1996. *Ecology*, 3rd ed. Blackwell Science, Oxford, UK.

Bond, W.J. & Midgley, G.F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biol.* 6: 865-869.

Bond W.J., Midgley G.F., Woodward F.I. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biol.* 9: 973-982.

Bruno, J. F., Stachowicz, J. J. & Bertness, M. D. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18: 119-125.

Callaway, R.M. 1995. Positive interactions among plants. *Bot. Rev.* 61: 306-349.

Cabral, A.C., De Miguel, J.M., Rescia, A.J., Schmitz, M.F. & Pineda, F.D. 2003. Shrub encroachment in Argentinean savannas. *J. Veg. Sci* 14: 145-152.

Colautti, R.I., Grigorovitch, I.A. & MacIsaac, H.J. 2006. Propagule pressure: a null model for biological invasions. *Biol. Invas.* 8: 1023-1037.

Cook, W.M., Yao, J., Foster, B.L., Holt, R.D. 4 & Patrick, L.B. 2005. Secondary succession in an experimentally fragmented landscape: community patterns across space and time. *Ecology* 86: 1267-1279.

Coomes, D.A. & Grubb, P.J. 2003. Colonization, tolerance, competition and seed-size variation within functional groups. *Trends Ecol. Evol.* 18: 283-291.

Dalling J.W. & Hubbell S.P. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *J. Ecol.* 90: 557–568.

Desdevises, Y., Legendre, P., Azouzi, L. & Morand, S. 2003. Quantifying phylogenetically structured environmental variation. *Evolution* 57: 2647-2652.

Duarte, L.S., Dos Santos, M.M.G., Hartz, S.M. & Pillar, V.D. 2006a. Role of nurse plants on *Araucaria* Forest expansion over grassland in south Brazil. *Aust. Ecol.* 31: 520-528.

Duarte, L.S., Machado, R.E., Hartz, S.M. & Pillar, V.D. 2006b. What saplings can tell us about forest expansion over natural grasslands. *J. Veg. Sci.* 17: 799-808.

Éhrlen, J. & Eriksson, O. 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81:1667-1674.

Fargione, J., Brown, C.S. & Tilman, D. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. USA* 100: 8916-8920.

Fontoura, S.B.; Ganade, G. & Larocca, J. 2006. Changes in plant community diversity and composition across an edge between Araucaria forest and pasture in South Brazil. *Rev. Bras. Bot.* 29:79-91.

Foster, S. & Janson, C.H. 1985. The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* 66: 773-780.

Gauthier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. & Thiollay, J.M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.

Harper, J.L.; Lovell, P.H. & Moore, K.G. 1970. The shapes and sizes of seeds. *Annu. Rev. Ecol. Syst.* 1:327-356.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.

Hubbell, S.P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography.* Princeton University Press, Princeton, US.

Hubbell, S.P. 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Func. Ecol.* 19: 166–172.

Jakobsson A. & Eriksson O. 2000. A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* 88: 494-502.

Jordano, P. 1995 Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *Am. Nat.* 145: 163-191.

Kelly, C.K. 1995. Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia* 102: 377-388.

Kelly, C.K. & Purvis A. 1993. Seed size and establishment conditions in tropical trees: On the use of taxonomic relatedness in determining ecological patterns. *Oecologia* 94: 356-360.

Kidson, R. & Westoby, M. 2000. Seed mass and seedling dimensions in relation to seedling establishment. *Oecologia* 125: 11-17.

Klein, R.M. 1960. O aspecto dinâmico do pinheiro brasileiro. *Sellowia* 12: 17-51.

Kunin, W.E. 1998. Biodiversity at the edge: A test of the importance of spatial ‘‘mass effects’’ in the Rothamsted Park Grass experiments *Proc. Natl. Acad. Sci. USA* 95: 207–212.

Legendre, P. & Legendre, L. 1998 *Numerical Ecology,* 2nd ed. Elsevier, Amsterdam, The Netherlands.

Leishman, M. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93: 294-302.

Leishman, M. & Murray, B.R. 2001. The relationship between seed size and abundance in plant communities: model predictions and observed patterns. *Oikos* 94: 151-161.

Leishman, M., Wright, I.J., Moles, A.T. & Westoby, M. 2000. The evolutionary ecology of seed size. In: Fenner, M. (ed.) *Seeds: The Ecology of Regeneration in Plant Communities*, 2nd. p. 31-57. CAB International, Wallingford, UK.

Lockwood, J.L., Cassey P. & Blackburn, T. 2005 The role of propagule pressure in explaining species invasions. *Trends Ecol. Evol.* 20: 223-228.

MacArthur, R.H. & Wilson, E.O. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, US.

Machado, R.E. 2004. *Padrões Vegetacionais em Capões de Floresta com Araucaria no Planalto Nordeste do Rio Grande do Sul, Brasil*. MSc. Thesis, UFRGS, Porto Alegre, Brazil.

Mack, A. 1998. An advantage of large seed size: tolerating rather than succumbing to seed predators. *Biotropica* 30: 604-608.

Moles, A.T., Ackerly, D.D., Webb, C.O., Tweddle, J.C., Dickie, J.B. & Westoby, M. 2005. A brief history of seed size. Science 307: 576-580.

Moles, A.T., Warton, D.I. & Westoby, M. 2003. Do small-seeded species have higher survival through seed predation than large-seeded species? *Ecology* 84: 3148–3161.

Moles, A. & Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. *J. Ecol.* 92: 372-383.

Moles, A. & Westoby, M. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113:91-105.

Moreno, J.A. 1961. *Clima do Rio Grande do Sul*. Secretaria da Agricultura do RS, Porto Alegre, Brazil.

Nathan, R. & Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15: 278-285.

Oliveira, J.M. & Pillar V.D. 2004. Vegetation dynamics on mosaics of *Campos* and Araucaria forest between 1974 and 1999 in Southern Brazil. *Comm. Ecol.* 5: 197-202.

Pedó, E. 2005. *Comunidade de Pequenos Mamíferos Não-voadores em Áreas de Ecótono Campo-floresta com Araucária na Região dos Campos de Cima da Serra, Rio Grande do Sul*. MSc Thesis, UFRGS, Porto Alegre, Brazil.

Pillar, V.D. 2006. *MULTIV; Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling; User's Guide v. 2.4.* Departamento de Ecologia, UFRGS, Porto Alegre, Brazil (software and manual available from http://ecoqua.ecologia.ufrgs.br).

Pillar V.D. & Orlóci, L. 1996. On randomization testing in vegetation science: multifactor comparisons of relevé groups. *J. Veg. Sci.* 7:585-592.

Rambo, B. 1951. O elemento andino no pinhal riograndense. *Anais Botânicos do HBR* 3: 7-39.

Rambo, B. 1994. *A Fisionomia do Rio Grande do Sul*. 3rd ed., Ed. Unisinos, São Leopoldo, Brazil.

Ridley, H.N. 1930. *The Dispersal of Plants Throughout the World*. L Reeve and Co, Kent, UK.

Schelhas, R. & Greenberg, J. 1996. *Forest Patches in Tropical Landscapes*. Island Press, Washington, US.

Scholes, R.J., Archer, S.R. 1997. Tree-grass interactions in savannas. *Ann. Rev. Ecol. Syst.* 28: 517-544.

Sokal, R.R. & Rohlf, F.J. 1981. *Biometry* 2nd ed. W.H. Freeman & Co., San Francisco, US.

Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proc. Natl. Acad. Sci. USA* 30: 10854-10861.

Turnbull, L.A., Rees, M. & Crawley, M.J. 1999. Seed mass and the competition/colonization trade-off: a sowing experiment. *J. Ecol.* 87: 899-912.

Van der Pijl, L. 1982. *Principles of Dispersal in Higher Plants*. Springer-Verlag, Berlin, Germany.

Venable, D.L. 1996. Packing and provisioning in plant reproduction. *Phil. Trans. R Soc. London B.* 351: 1319-1329.

Vieira, E.M., Pizo, M.A. & Izar, P. 2003. Fruit and seed exploitation by small rodents of the Brazilian Atlantic forest. *Mammalia* 67: 1-7

Westoby, M.; Rice, B. & Howell, J. 1990. Seed size and plant growth as factors in dispersal spectra. *Ecology* 71: 1307-1315.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Ann. Rev. Ecol. Syst.* 33: 125-159.

Wheelwright, N.T. 1985. Fruit size, gape width and the diets of fruit-eating birds. *Ecology* 66: 808-818.

Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *J. Ecol.* 62: 417-428.

Table 1. Linear multiple regression model of log species frequency in *Araucaria* forest patches (dependent variable, obtained from matrix C) on seed size and seed number (independent variables, from matrix D_1). All variables were centralized and standardized. The independent variables were residuals of linear multiple regressions of seed size and seed number on phylogeny (matrix F) and DAT (matrix D_2) ($R^2 = 0.31$; $F_{2,35} = 7.72$; $P < 0.01$). β: Standardized regression coefficient; SE: standard error of the β coefficient; VIF: variance inflation factor, a measure of multicollinearity among independent variables (1 = maximum independence among variables). The intercept is zero.

Descriptor variable	β	SE	t	*P*	VIF
Seed size	– 0.38	0.14	-2.72	0.01	1.00
Seed number	0.40	0.14	2.86	<0.01	1.00

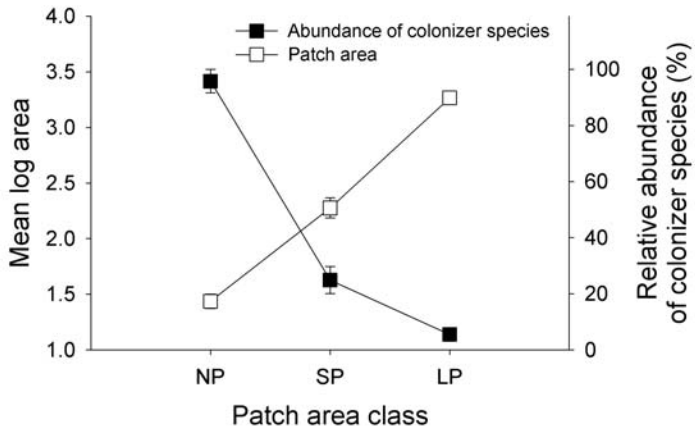

Fig. 1. *Relationship between patch area and the abundance of colonizer species in* Araucaria *forest patches in southern Brazil (adapted from Duarte et al. 2006b). Values are means* ± *standard errors. NP: Nurse plants; SP: Small patches; LP: Large patches. The abundance of colonizer species in patches estimates the probability* m *of a dead sapling being replaced by a new colonizer species (Hubbell 2001).*

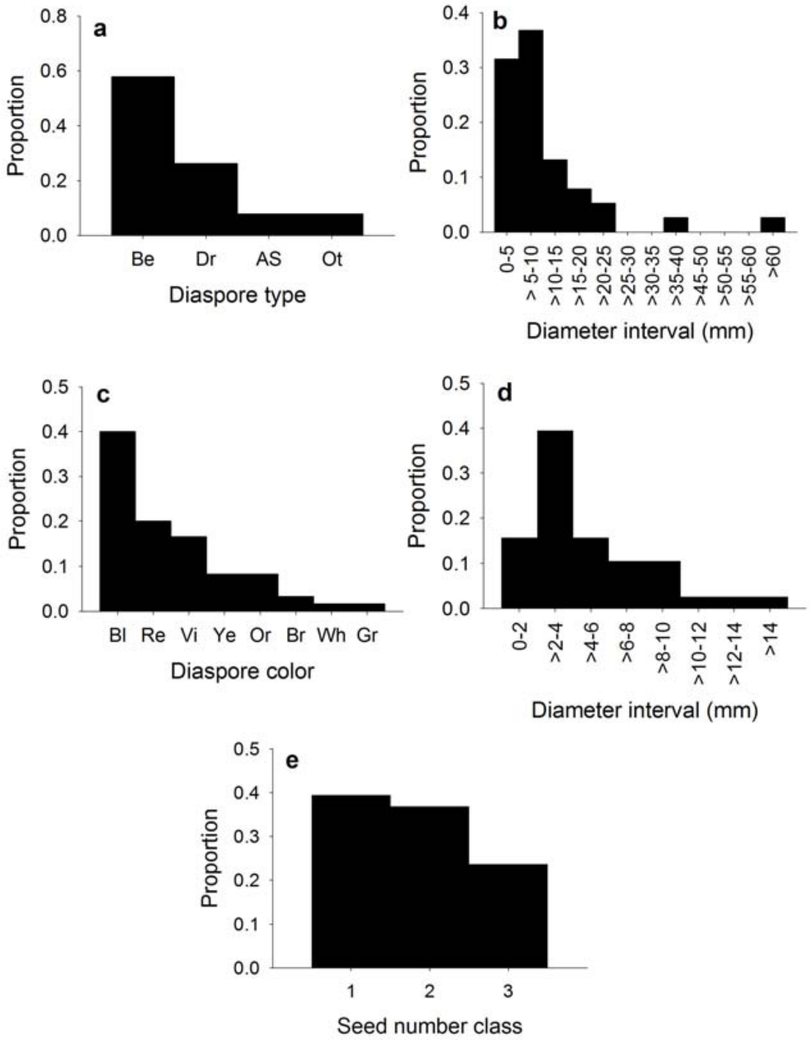

Fig. 2. *Diaspore traits of woody sapling species colonizing* Araucaria *forest patches in southern Brazil. a) Diaspore type. Be: Berry; Dr: Drupe; AS: Arillate seed; Ot: Others. b) Diaspore size. c) Diaspore color. Bl: Black; Re: Red; Vi: Violet; Ye: Yellow; Or: Orange; Br: Brown; Wh: White; Gr: Green. d) Seed size. e) Seed number per diaspore. 1: single-seeded; 2: two to five seeds; 3: more than five seeds.*

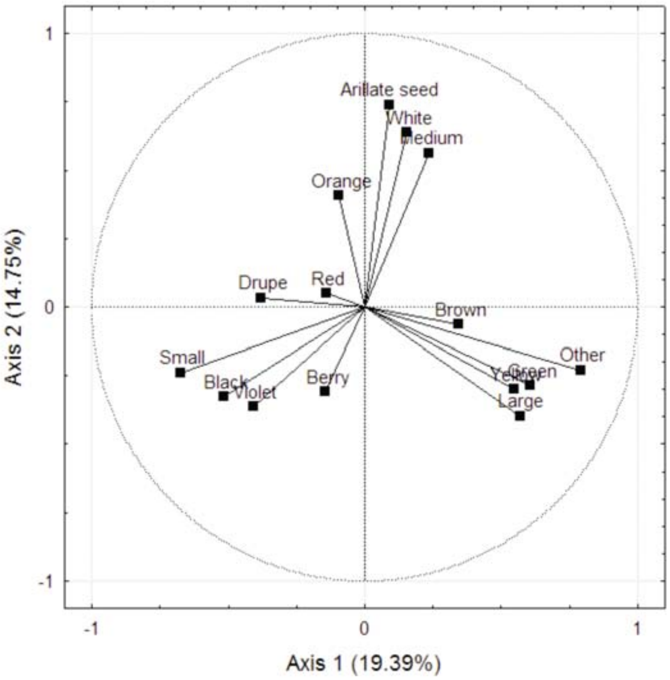

Fig. 3. *Projection of diaspore traits related to disperser attraction (DAT, matrix* $\mathbf{D}_2$*) on the PCA axes 1 and 2. Variables significantly correlated with axis 1: Diaspore type: Other and Drupe; Diaspore size: Large and Small; Diaspore color: Green, Yellow, Brown, Violet and Black. Variables significantly correlated with axis 2: Diaspore type: Arillate seed and Berry; Diaspore size: Medium and Large; Diaspore color: White, Orange, Green, Yellow, Black and Violet.*

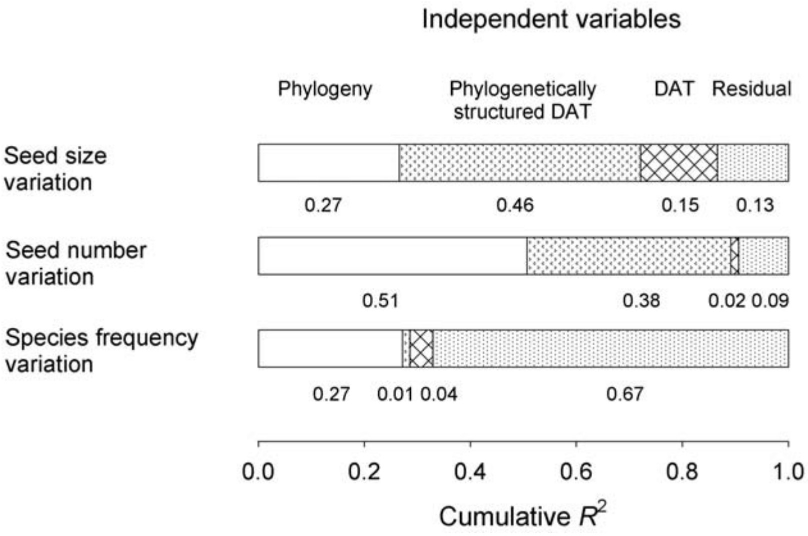

Fig. 4. *Partitioning of the species level variation of seed size, seed number (both from matrix* $\boldsymbol{D}_1$*) and log species frequency (from matrix* ***C****) among phylogeny (matrix* ***F****), disperser attraction traits (DAT, matrix* $\boldsymbol{D}_2$*), phylogenetically structured DAT, and unexplained variation components. Horizontal lines represent the total variation, expressed by the coefficient of determination* R^2*, observed in the dependent variables. Numbers below bars are the proportions of the variation explained by each independent variable.*

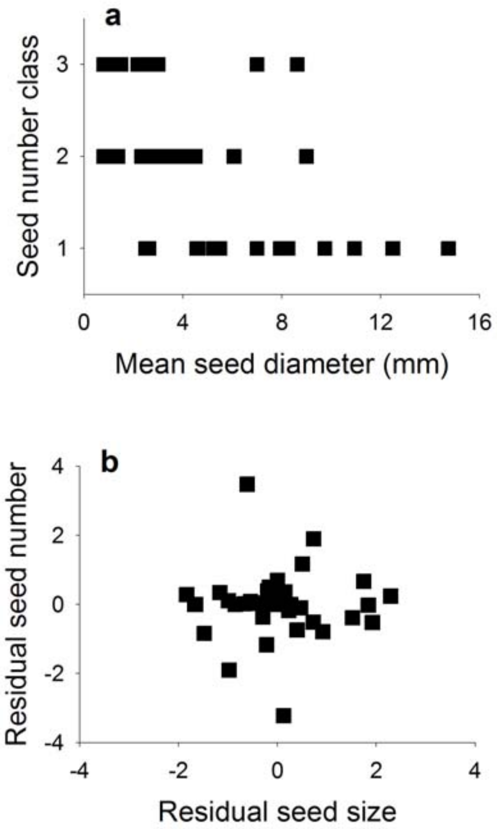

Fig. 5. *Relationship between seed size and number in woody plant species colonizing* Araucaria *forest patches in southern Brazil. a) raw variables from matrix* $\boldsymbol{D}_1$ *(*r = *-0.48,* P < *0.01). b) Residuals of a regression on PCA scores of phylogeny (matrix* $\boldsymbol{F}$*) and disperser attraction traits (DAT, matrix* $\boldsymbol{D}_2$*) (*r = < *0.01,* P = *0.96).* P *values generated by randomization (10000 iterations).*

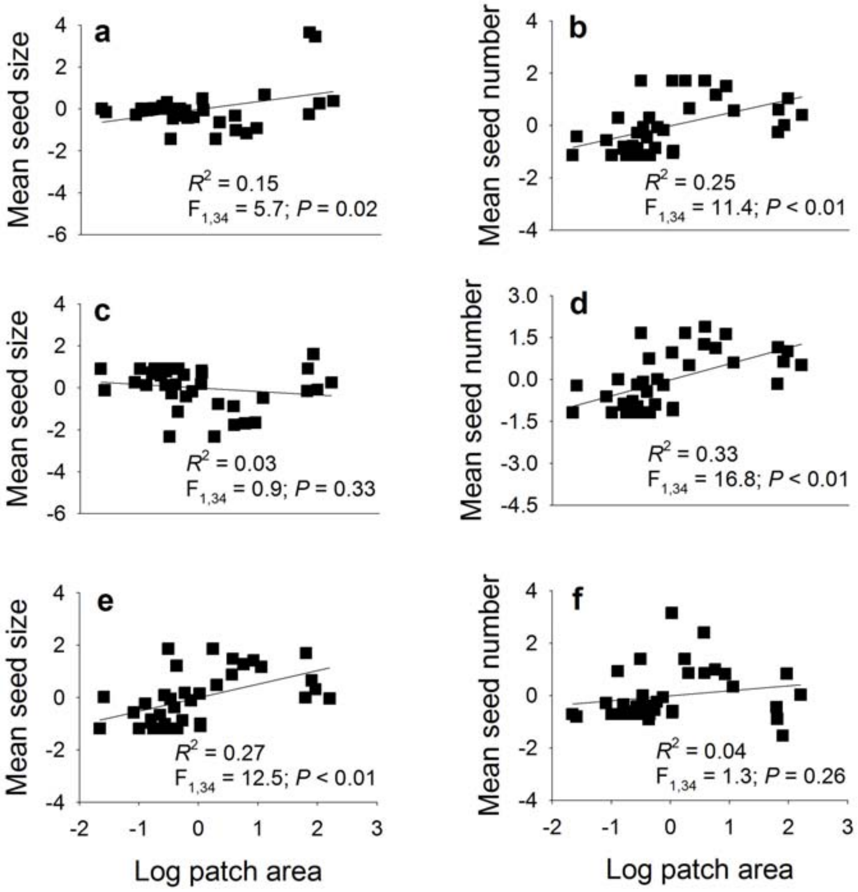

Fig. 6. *Seed size and seed number variation at community level in woody plants colonizing* Araucaria *forest patches of different sizes in southern Brazil. Figures* a *and* b *show, respectively, variation of seed diameter and seed number mean values (raw data) as explained by patch area. Figures* c *and* d *show, respectively, variation of mean seed diameter and seed number predicted by phylogeny, DAT and phylogenetically structured DAT as a function of patch area. Figures* e *and* f *show, respectively, the residual variation of mean seed diameter and seed number values, after the removal of phylogeny, DAT and phylogenetically structured DAT effects, as a function of patch area. Prior to regression all variables were centralized and standardized by the standard deviation.*

Appendix 1.

Ecological status and diaspore traits of woody species occurring in *Araucaria* forest patches in southern Brazil.

Species	Abbrev.[a]	Status[b]	Diaspore traits			Seed traits	
			Type[c,h]	Size[d,h]	Color[e,h]	Size[e,h]	Number[f,h]
ANNONACEAE							
Rollinia rugulosa	Roru	Col	C	65.0	Y or G	8.6	3
AQUIFOLIACEAE							
Ilex dumosa	Ildu	Res/Col	D	3.0	Bl	2.4	2
Ilex microdonta	Ilmi	Res/Col	D	5.0	R, V or Bl	2.7	2
Ilex paraguariensis	Ilpa	Col	D	5.0	R, V or Bl	3.2	2
ERYTHROXYLACEAE							
Erythroxylum cuneifolium	Ercu	Col	D	5.5	O or Bl	5.2	1
FABACEAE							
Inga lentiscifolia	Inle	Col	P	35.8	Br	7.0	3
LAMIACEAE							
Vitex megapotamica	Vime	Col	D	16.3	V or Bl	9.0	2
LAURACEAE							
Nectandra grandiflora	Negr	Col	B	13.3	Bl	9.8	1
Ocotea corymbosa	Occo	Col	B	7.5	Bl	5.5	1
Ocotea elegans	Ocel	Col	B	12.5	Bl	7.0	1
Ocotea indecora	Ocin	Col	B	15.3	Bl	8.0	1
Ocotea porosa	Ocpo	Col	B	15.5	Bl	14.8	1
Ocotea puberula	Ocpb	Col	B	9.5	R or V	5.3	1
MELASTOMATACEAE							
Leandra laevigata	Lela	Col	B	3.0	V or Bl	0.8	3
Leandra sublanata	Lesu	Col	B	3.5	V or Bl	0.9	3
Miconia hyemalis	Mihy	Res/Col	B	3.0	V or Bl	1.5	3
Miconia sellowiana	Mise	Col	B	3.0	Y, V or Bl	1.4	2

Appendix 1. Cont.

MELIACEAE							
Cabralea canjerana	Caca	Col	A	8.3	O or R*	8.3	1
MONIMIACEAE							
Mollinedia elegans	Moel	Col	D	5.0	Bl	4.6	1
MORACEAE							
Ficus luschnatiana	Filu	Col	F	10.0	Y	1.0	3
MYRSINACEAE							
Myrsine coriacea	Myco	Col	D	3.0	Bl	2.6	1
Myrsine lorentziana	Mylo	Res/Col	D	3.4	Bl	2.6	1
MYRTACEAE							
Calyptranthes grandifolia	Cagr	Col	B	10.0	R or V	6.1	2
Eugenia uruguayensis	Euur	Col	B	11.0	Y, R or Bl	11.0	1
Myrceugenia euosma	Myeu	Res/Col	B	8.0	Bl	3.0	2
Myrceugenia miersiana	Mymi	Col	B	9.8	O or Bl	4.5	2
Myrceugenia myrcioides	Mymy	Col	B	15.0	V or Bl	0.8	2
Myrcia hartwegiana	Myha	Col	B	8.0	R or Bl	3.8	2
Psidium cattleyanum	Psca	Col	B	22.5	Y or R	3.0	3
Siphoneugena reitzii	Sire	Res/Col	B	7.0	R or Bl	4.0	2
RUBIACEAE							
Rudgea parquioides	Rupa	Col	D	6.5	R	3.5	2
RUTACEAE							
Zanthoxylum rhoifolium	Zarh	Col	A	4.0	Bl*	2.5	1
SALICACEAE							
Xylosma pseudosalzmanii	Xyps	Col	B	7.0	R	2.3	2
SAPINDACEAE							
Matayba elaeagnoides	Mael	Col	A	12.5	W*	12.5	1
SOLANACEAE							
Solanum johannae	Sojo	Col	B	25.0	?	2.2	3
Solanum variabile	Sova	Col	B	8.0	O	2.5	3

Appendix 1. Cont.

THYMELAEACEAE							
Daphnopsis fasciculata	Dafa	Res/Col	D	5.0	O	4.6	1
WINTERACEAE							
Drimys brasiliensis	Drbr	Res/Col	B	6.0	Bl	2.8	2

[a] Abbreviated species names

[b] Status: Res – Always resident; Col – Always colonizer; Res/Col – Resident in some patches and colonizer in others.

[c] Diaspore types: A) Arillate seed, B) Berry, C) Compound fruit, D) Drupe, F) Fig, G) Gimnosperm diaspore, P) Pod

[d] Mean diaspore diameter, in mm

[e] Bl) Black, Br) Brown, G) Green, O) Orange, R) Red, V) Violet, Y) Yellow, W) White, * aril color

[f] Mean seed diameter, in mm

[g] Seed number classes: 1) single seed; 2) two to five seeds; 3) more than five seeds

[h] References: Abramides et al. (2002), Albuquerque (1985), Amaral Jr. (1980), Backes & Irgang (2002, 2004), Barroso et al. (1999), Burkart (1979), Cabrera et al. (1965), Cabrera & Zardini (1978), Carauta & Diaz (2002), Carvalho (2003), Coe-Teixeira (1980), Correa (1984a,b), Dillenburg (1978, 1985), Edwin & Reitz (1967), Jung-Mendaçolli & Bernacci (1997), Klein & Sleumer (1984), Lahitte et al. (1999), Landrum (1981), 22) Legrand & Klein (1967, 1969, 1970, 1971, 1977), Lima & Guedes-Bruni (2004), Lorenzi (1998, 2000), Marchiori (1997), Marchiori & Sobral (1997), Martinez (1997), Martius (1886-1888), Mattos (1983, 1984), Mentz & Oliveira (2004), Nevling Jr & Reitz (1968), New York Botanical Garden (2006), Pastore (1997), Pedralli (1982), Peixoto (1979, 2001), Possamai (1997), Proença (1990), Quinet & Andreata (2002), Reitz

et al. (1988), Rohwer (1993), Rosa (1997), Rossoni (2003), Sanchotene (1985), Smith & Downs (1957), Sobral (1987, 2003), Suarez et al. (1965), Trinta & Santos (1997), Vattimo (1956), Zachia & Irgang (2004)

References

Abramides, P.L.G., Bernacci, L.C., Torres, R.B. & Mendaçolli, S.L.J. 2002. Herbário do Instituto Agronômico IAC. Available on http://200.136.175.14.

Albuquerque, B.W.P. 1985. *Flora do Estado de Goiás - coleção Rizzo, Rutaceae*. Ed UFG, Goiânia, Brazil.

Amaral Jr., A. 1980. *Flora Ilustrada Catarinense - Eritroxiláceas*. Herbário Barbosa Rodrigues, Itajaí, Brazil.

Anon. 2006. *New York Botanical Garden Virtual Herbarium - Catalog of Vascular Plants*. Available on http://sciweb.nybg.org/science2/hcol/allvasc/index.asp

Backes, P. & Irgang, B.E. 2002. *Árvores do Sul*. Instituto Souza Cruz, Santa Cruz do Sul, Brazil.

Backes, P. & Irgang, B.E. 2004. *Mata Atlântica – As Árvores e a Paisagem*. Ed Paisagem do Sul, Porto Alegre, Brazil.

Barroso, G.M., Morim, M.P., Peixoto, A.L. & Ichaso, C.L.F. 1999. *Frutos e Sementes - Morfologia Aplicada à Sistemática de Dicotiledôneas*. Editora UFV, Viçosa, Brazil.

Burkart, A. 1979. *Flora Ilustrada Catarinense - Leguminosas*. CNPq, IBDF, Herbario Barbosa Rodrigues, Itajaí, Brazil.

Cabrera, A.L., Correa, M.N., Dawson, G., Fabris, H.A., Krapovickas, A. & Pontiroli, A. 1965. *Flora de la Província de Buenos Aires, Oxalidáceas a Umbelíferas*. INTA, Buenos Aires, Argentina.

Cabrera, A.L. & Zardini, E.M. 1978. *Manual de la Flora de los Alrededores de Buenos Aires* 2nd edn. Editorial ACME SACI, Buenos Aires, Argentina.

Carauta, J.P.P. & Diaz, B.E. 2002. *Figueiras no Brasil*. Editora UFRJ, Rio de Janeiro, Brazil.

Carvalho, P.E.R. 2003. *Espécies Arbóreas Brasileiras vol 1*. EMBRAPA, Colombo, Brazil.

Coe-Teixeira, B. 1980. Lauráceas do gênero *Ocotea* no Estado de São Paulo. *Rodriguésia* 32: 55-190.

Correa, M.P. 1984a. *Dicionário das Plantas Úteis do Brasil e das Exóticas Cultivadas vol I*. Ministério da Agricultura, IBDF, Brasília, Brazil.

Correa, M.P. 1984b. *Dicionário das plantas úteis do Brasil e das exóticas cultivadas vol III*. Ministério da Agricultura, IBDF, Brasília, Brazil.

Dillenburg, C.R. 1978. *A Tribo Psychotrieae (Rubiaceae) no Rio Grande do Sul*. MSc Thesis, UFRGS, Porto Alegre, Brazil.

Dillenburg, C.R. & Porto, M.L. 1985. Flora ilustrada do Rio Grande do Sul – Rubiaceae, tribo Psychotrieae. *Bol. Inst. Biociênc.* 39: 1-76.

Edwin, G. & Reitz, R. 1967. *Flora Ilustrada Catarinense - Aquifoliáceas*. CNPq, IBDF, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Jung-Mendaçolli, S.L. & Bernacci, L.C. 1997. Myrsinaceae. In Melo, M.M.R.F., Barros, F., Chiea, S.A.C., Kirizawa, M., Jung-Mendaçolli, S.L. & Wanderley, M.G.L. (eds). *Flora fanerogâmica da Ilha do Cardoso*. pp 81-98. Instituto de Botânica, São Paulo, Brazil.

Klein, R.M. & Sleumer, H.O. 1984. *Flora Ilustrada Catarinense - Flacourtiáceas*. CNPq, IBDF e Herbário Barbosa Rodrigues, Itajaí, Brazil.

Lahitte, H.B., Hurrell, J.A., Haloua, M.P., Jankowski, L.S. & Belgrano, M.J. 1999. *Trees of the Río de La Plata*. L.O.L.A, Buenos Aires, Argentina.

Landrum L.R. 1981. *Flora Neotropica - A Monograph of the Genus Myrceugenia (Myrtaceae).* The New York Botanical Garden, New York, USA.

Legrand, C.D. & Klein, R.M. 1967. *Flora Ilustrada Catarinense – Mirtáceas*, pp 1-44. CNPq, IBDF, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Legrand, C.D. & Klein, R.M. 1969. *Flora Ilustrada Catarinense – Mirtáceas*, pp 45-216. CNPq, IBDF, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Legrand, C.D. & Klein, R.M. 1970. *Flora Ilustrada Catarinense – Mirtáceas*. CNPq, IBDF, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Legrand, C.D. & Klein, R.M. 1971. *Flora Ilustrada Catarinense – Mirtáceas*. CNPq, IBDF, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Legrand, C.D. & Klein, R.M. 1977. *Flora Ilustrada Catarinense – Mirtáceas*. CNPq, IBDF, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Lorenzi, H. 1998. *Árvores Brasileiras Vol. 2* 2nd edn. Ed Plantarum, São Paulo, Brazil.

Lorenzi, H. 2000. *Árvores Brasileiras Vol. 1* 3rd edn. Ed Plantarum, São Paulo, Brazil.

Marchiori, J.N.C. 1997. *Dendrologia das Angiospermas - das Magnoliáceas às Flacurtiáceas*. Ed UFSM, Santa Maria, Brazil.

Marchiori, J.N.C. & Sobral, M. 1997. *Dendrologia das Angiospermas - Myrtales*. Ed UFSM, Santa Maria, Brazil.

Martinez, R.V. 1997. *Flórula de las Reservas Biológicas de Iquitos, Peru (Allpahuayo-Mishana, Explornapo, Explorama Lodge)*. The Missouri Botanical Garden Press, St Louis, USA.

Martius, C.F.P. 1886-1888. *Flora Brasiliensis, Melastomataceae*. Monach, Leipzig, Germany.

Mattos, J.R. 1983. Myrtaceae do Rio Grande do Sul. *Roessleria* 5: 163-359.

Mattos, J.R. 1984. Myrtaceae do Rio Grande do Sul. *Roessleria* 6: 3-394.

Mentz, L.A. & Oliveira, P.L. 2004. *Solanum* (Solanaceae) na região sul do Brasil. *Pesquisas (Sér Bot)* 54: 1-327.

Nevling Jr., L.I. & Reitz, R. 1968. *Flora Ilustrada Catarinense - Timeleáceas*. CNPq, IBDF, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Pastore, J.A. 1997. Meliaceae. In Melo, M.M.R.F., Barros, F., Chiea, S.A.C., Kirizawa, M., Jung-Mendaçolli, S.L. & Wanderley, M.G.L. (eds). *Flora fanerogâmica da Ilha do Cardoso*. pp 57-67. Instituto de Botânica, São Paulo, Brazil.

Pedralli, G. 1982. *A família Lauraceae Lindley no Rio Grande do Sul, Brasil*. MSc Thesis, UFRGS, Porto Alegre, Brazil.

Peixoto, A.L. 1979. Contribuição ao conhecimento da seção Exappendiculatae Perkins do gênero Mollinedia Ruiz et Pavon (Mollinedieae, Monimoideae, Monimiaceae). *Rodriguésia*. 31: 135-222.

Possamai, R.M. 1997. *Guia ilustrado da flora arbórea do Morro do Osso, Porto Alegre, RS*. Graduation Thesis, UFRGS, Porto Alegre, Brazil.

Proença, C.E.B. 1990. A revision of *Siphoneugena* (Berg). *Edinburgh J. Bot.* 47: 239-271.

Quinet, A. & Andreata, R.H.P. 2002. Lauraceae Jussieu na Reserva Ecológica de Macaé de Cima, Município de Nova Friburgo, Rio de Janeiro, Brasil. *Rodriguésia* 53: 59-121.

Reitz, R., Klein, R.M. & Reis, A. 1988. *Projeto Madeira do Rio Grande do Sul*. Herbário Barbosa Rodrigues, Itajaí, Brazil.

Rohwer, J.G. 1993. *Flora Neotropica: Lauraceae – Nectandra*. The New York Botanical Garden, New York, USA.

Rosa, F.F. 1997. *Contribuição ao conhecimento das comunidades vegetais da Planície de Inundação do Rio dos Sinos, RS*. MSc Thesis, UFRGS, Porto Alegre, Brazil.

Rossoni, M.G. 2003. *Fenologia de espécies arbóreas e arbustivas em fragmento de Floresta Ombrófila Densa, Municipio de Dom Pedro de Alcântara, RS - Brasil*. Doctor Thesis, UFRGS, Porto Alegre, Brazil.

Sanchotene, M.C.C. 1985. *Frutíferas Nativas Úteis a Fauna na Arborização Urbana*. Editora Feplam, Porto Alegre, Brazil.

Smith, L.B. & Downs, R.J. 1957. Resumo preliminar das Myrsináceas de Santa Catarina. *Sellowia* 8: 237-248.

Sobral, M. 1987. *Erythroxylum* (Erythroxylaceae) no Rio Grande do Sul. *Pesquisas (Sér Bot)* 38: 7-42.

Sobral, M. 2003. *A Família das Myrtaceae no Rio Grande do Sul*. Ed Unisinos, São Leopoldo, Brazil.

Suarez, D.A., Bacigalupo, N.M., Cabrera, A.L., Dawson, G., Fabris, H.A., Crovetto, R.M., Pontiroli, A. & Troncoso, N.S. 1965. *Flora de la Província de Buenos Aires*. INTA, Buenos Aires, Argentina.

Trinta, E.F. & Santos, E. 1997. *Flora Ilustrada Catarinense - Winteráceas*. Petrobras, Herbário Barbosa Rodrigues, Itajaí, Brazil.

Vattimo, I. 1956. O Gênero *Ocotea* Aubl. no Sul do Brasil. *Rodriguésia* 18-19: 265-349.

Zachia, R.A. & Irgang, B.E. 2004. A família Annonaceae no Estado do Rio Grande do Sul, Brasil. *Pesquisas (Bot)* 55: 7-127.

Capítulo 5. Plant diaspore types as indicators of mutualistic interactions in woody vegetation patches developing into a grassland-forest mosaic[4]

Duarte, Leandro da S.[1*]; Carlucci, Marcos B.[1,3]; Fontana, Carla S.[2,4]; Hartz, Sandra M.[1,5] & Pillar, Valério D.[1,6]

[1]*Departamento de Ecologia, Universidade Federal do Rio Grande do Sul, CP 15007, Porto Alegre, RS 91501-970, Brazil;*

[2]*Museu de Ciências Naturais, Pontifícia Universidade Católica do rio Grande do Sul, Av. Ipiranga 6681, Porto Alegre, RS 90619-900, Brazil;*

[3]*E-mail: marcos.carlucci@ufrgs.br,* [4]*E-mail: carla@pucrs.br,* [5]*E-mail: sandra.hartz@ufrgs.br,* [6]*E-mail: vpillar@ufrgs.br;*

[*]*Corresponding author*; *Fax +55 5133087626; E-mail leandro.duarte@ufrgs.br; duarte.ldas@gmail.com*

Resumo

Questões: 1) A proporção de plantas colonizadoras dispersas por vertebrados varia durante a colonização de manchas florestais de diferentes tamanhos?; 2) Qual é a influência da filogenia na alocação de espécies colonizadoras em tipos de diásporos definidos por atributos relacionados à

---

[4] Artigo submetido à publicação no periódico *Journal of Vegetation Science em 15 de junho de 2007.*

atração de dispersores (DAT)?; 3) Tipos de diásporos variam em relação ao número de interações com diferentes aves consumidoras de frutos?, 4) Há uma associação funcional entre DAT de diásporos de plantas lenhosas colonizadoras e atributos ecológicos de aves consumidoras de diásporos durante a colonização de manchas de floresta com *Araucaria* de tamanhos diferentes?

Local: Um mosaico de campos e floresta com *Araucaria* em São Francisco de Paula, Rio Grande do Sul, Brasil (29°28'S and 50°13'W).

Métodos: Manchas florestais de tamanhos diferentes num sítio campestre recuperando-se há 10 anos de distúrbios antrópicos foram amostradas pela ocorrência de plantas lenhosas jovens residentes e colonizadoras. A proporção de espécies colonizadoras dispersas por vertebrados em manchas de diferentes tamanhos foi comparada através de ANOVA com teste de aleatorização. Além disso, nós descrevemos espécies colonizadoras de acordo com relações filogenéticas e DAT dos diásporos (tipo, tamanho e cor dos diásporos). Então, nós classificamos (WPGMA) as plantas colonizadoras de acordo com DAT, o que foi feito em nível de família para minimizar a influência da filogenia sobre DAT (filogenia e DAT foram significativamente independentes um do outro em nível de família). Também, nós obtivemos dados sobre registros de frugivoria envolvendo plantas colonizadoras e aves consumidoras de frutos, as quais foram caracterizadas em relação ao tamanho do corpo, uso do habitat e dieta. Finalmente, nós usamos ordenação das manchas por tipos de diásporos definidos por DAT para avaliar padrões de interações entre plantas e aves em nível de comunidade.

Resultados: 1) A maioria das espécies lenhosas colonizando manchas de floresta com *Araucaria* apresentaram diásporos com atributos associados com dispersão por vertebrados. Em manchas pequenas e grandes a proporção de espécies dispersas por vertebrados foi menor do que sob plantas-berçário, e não diferiu entre si. 2) Quatro tipos nítidos de diásporos definidos por DAT foram encontrados. 3) O número de interações com aves consumidoras não diferiu entre distintos grupos de diásporos definidos por DAT. 4) Diásporos do tipo B foram associados com plantas-berçário, enquanto os tipos A, C e D relacionaram-se com manchas pequenas e grandes. Interações entre plantas e frugívoros envolvendo aves de tamanho médio, a maioria frugívoras, associadas com habitats de borda e apresentando hábito migratório correlacionaram-se positivamente com manchas pequenas e grandes, enquanto aquelas envolvendo aves residentes de tamanho grande, em sua maioria não-frugívoras e habitantes de áreas abertas e florestas associaram-se com plantas-berçário.

Conclusões: Avaliando os níveis taxonômicos que maximizaram a independência de clados em relação a DAT, nós pudemos detectar as unidades mais apropriadas para comparações interespecíficas envolvendo plantas colonizadoras. Diásporos do tipo B associaram-se com um amplo espectro de aves consumidoras de diásporos, tanto de uma perspectiva taxonômica quanto de uma perspectiva funcional, sugerindo que a colonização destes sítios dominados por gramíneas por plantas dispersas por vertebrados envolveu plantas generalistas em relação a dispersão. Diásporos dos tipos A, C e D (associados com manchas pequenas e grandes) apresentaram interações mais restritas a aves frugívoras típicas. Nossos resultados indicaram um *trade-off* envolvendo a quantidade de reservas contidas na semente e a probabilidade do diásporo ser transportado por um frugívoro. Ou seja, se por uma perspeciva da planta uma semente maior representa mais reservas para a prole, então por uma perspectiva do dispersor o tamanho do diásporo poderia limitar seu manuseio pelo frugívoro, impedindo sua frutura dispersão.

Palavras-chave: Atributos de dispersão do diásporo, Teia de interações planta-frugívoro, Nucleação de manchas florestais, Colonização por plantas, Floresta com *Araucaria*, Planalto Sul-brasileiro

Abstract

Questions: 1) Does the proportion of vertebrate-dispersed colonizer plants vary during the colonization of forest patches of different sizes?; 2) What is the influence of phylogeny in the allocation of colonizer species into diaspore types defined by traits related to disperser attraction (DAT)?; 3) Do diaspore types vary in relation to number of interactions with different fruit-consumer birds?, 4) Is there a functional association between plant diaspore DAT of colonizer woody plants and ecological attributes of fruit-consumer birds during the colonization of *Araucaria* forest patches of different sizes?

Location: A mosaic of *Campos* grassland and *Araucaria* forest in São Francisco de Paula, Rio Grande do Sul, Brazil, at about 29°28'S and 50°13'W.

Methods: Forest patches of different sizes in a grassland site recovering for 10 years from human disturbances were surveyed by the occurrence of resident and colonizer woody plant saplings. The proportion of vertebrate-dispersed colonizer species in patches of different sizes was compared through ANOVA with randomization test. Further, we described colonizer species according to taxonomic phylogenetic relationships and diaspore DAT (diaspore type, size and color). Then, we classified (WPGMA) colonizer plants according to DAT, which was done at the family level to minimize the influence of phylogeny on DAT (phylogeny and DAT were significantly independent from each other at family level). Also, we obtained data on frugivory records involving colonizer plants and fruit-consumer birds, which were characterized in relation to body size, habitat use and diet. Finally, we used ordination of patches defined by DAT-defined diaspore types and plant-bird interaction patterns at the community level.

Results: 1) Most woody species colonizing *Araucaria* forest patches presented diaspores with attributes associated with dispersal by vertebrates. In small and large patches the proportion of vertebrate-dispersed species were lower than beneath nurse plants, and did not differ from each other. 2) Four sharp DAT-defined diaspore types were found. 3) The number of interactions with consumer birds did not differ among different DAT-defined diaspore types. 4) Type B diaspores were associated with nurse plants, while types A, C and D were related to small and large patches. Plant-frugivore interactions involving medium-sized birds, mostly frugivorous, associated with edge habitats and presenting a migrant habit were positively correlated with the small and large patches, while those involving large-sized resident birds, mostly non-frugivorous and open field/forest inhabitants were associated with nurse plants.

Conclusions: By evaluating the taxonomic levels that maximized the independence of clades in relation to DAT, we were able to detect the most suitable units for inter-specific comparisons involving colonizer plants. Type B diaspores were associated with a wide range of fruit-consumer birds, both from a taxonomic and a functional perspective, suggesting that the colonization of these grass-dominated sites by bird-dispersed plants involved dispersal-generalist plants. Types A, C and D diaspores (associated with small and large patches) showed interactions more restricted to typical frugivorous birds. Our results suggested a trade-off involving the amount of reserves contained in the seed and the probability of the diaspore being transported by a frugivore. That is to say, if from a plant perspective a larger seed represent more reserves for the offspring, then from the disperser perspective diaspore size might limit its handling by the frugivore, preventing its further dispersal.

Keywords Diaspore dispersal traits, plant-frugivore network, forest patch nucleation, plant colonization, *Araucaria* forest, southern Brazilian highlands

Abbreviations: CA = Correspondence Analysis, DAT = Diaspore traits related to disperser attraction.

Nomenclature: APG (2003), CBRO (2006), Anon. (2007)

Introduction

A tendency of woody plant encroachment in grass-dominated ecosystems has been currently observed in several parts of the world (Scholes & Archer 1997; Bond & Midgley 2000; Bond et al. 2003). In grassland-forest mosaics, isolated shrubs and trees modify the resource availability and environmental conditions beneath their crowns, creating suitable habitats for the establishment of forest species (e.g. Callaway 1995; Bruno et al. 2003), leading to the development of forest patches, a process Yarranton & Morrison (1974) have called *nucleation*.

Nucleation of forest patches in grassland depends on the dispersal of plant diaspores (namely fruits and/or seeds) from the forest to opens sites, and the mechanisms underlying this process provide the basis for the understanding of grassland-forest boundary dynamics. In woody plant communities exposed to high rainfall levels, a major proportion of plant species is dispersed by animals, especially vertebrates (Howe & Smallwood 1982; Herrera 2002), whose behavior and habitat preferences may determine the deposition site of seeds (Nathan & Muller-Landau 2000; Russo et al. 2006; Jordano et al. 2007). Woody plants established on grassland attract frugivorous birds that use them as perches for resting and/or foraging activities (Wunderle Jr. 1997; Toh et al. 1999; Shiels & Walker 2003), increasing seed rain beneath the plant crown, and thus favoring the colonization of open areas by forest species (Guevara et al. 1992; McClanahan & Wolfe 1993; Galindo-González et al. 2000; Slocum & Horwitz 2000; Holl 2002).

Traditionally, attributes of vertebrate-dispersed diaspores, like size, color and smell, have been used as indicators of dispersal by distinct disperser groups (e.g. birds v. mammals, see Ridley 1930; Howe and Smallwood 1982; Van der Pijl 1982; Janson 1983). Hereafter those diaspore traits are referred as DAT (disperser attraction traits). The adaptative value of DAT has been demonstrated in a variable extent by empirical studies (Knight & Siegfried 1983; Gauthier-

Hion et al. 1985; Wheelwright 1985; Tamboia et al. 1996; Rey et al. 1997; Bollen et al. 2004; Voigt et al. 2004), particularly where functional attributes of dispersers (e.g. body size, habitat use, diet) rather than its taxonomic affiliation (e.g. birds, mammals) were considered (Snow 1981; Gauthier-Hion et al. 1985; Zamora 2000; Dennis & Westcott 2006). Further, inter-specific variation in plant diaspore characteristics is highly related to phylogenetic affinities among species (Fischer & Chapman 1993). Indeed, phylogeny explains much of present-day ecological patterns, and its importance must not be underestimated (Westoby et al. 1995). However, incorporating phylogeny into ecological investigation introduces some theoretical and methodological problems. Species-based comparisons may overestimate the adaptive value of functional attributes if they constitute plesiomorphies, i.e. if they appeared first as evolutionary novelties in higher taxonomic levels (genus, families, etc.) rather than independently as convergent traits in each species of a given clade (i.e. apomorphies). In terms of plant-disperser interactions, straight diaspore-based classification of plants into dispersal syndromes is strongly influenced by phylogenetic affinities among species (Jordano 1995). Using higher taxonomic levels (genus, family, etc.) to define phylogeny-free diaspore types might prevent inflated co-variation in diaspore attributes due to plesiomorphic traits (Fischer & Chapman 1993; Voigt et al. 2004).

Vegetation mosaics formed by *Araucaria* forest and *Campos* grassland constitute the main natural landscape found in southern Brazilian highlands (Rambo 1994). *Araucaria* forest expansion over grassland in southern Brazil was already demonstrated by paleopollen evidence (Behling 2002; Behling & Pillar 2007), either gradually by edge dynamics (Oliveira & Pillar 2004), or by nucleation of forest patches in the grassland (Klein 1960; Duarte et al. 2006a). Recently we found that in *Araucaria* forest patches released for ten years from burning and cattle grazing disturbances the recruitment of woody saplings was strongly associated with patch area (Duarte et al. 2006b). Isolated *Araucaria angustifolia* individuals scattered in the grassland act as nurse plants, promoting the establishment of colonizer forest species (Duarte et al. 2006a). In small patches, consisting of few adult trees (capable to recruit resident saplings) plus a variable amount of woody saplings mixed to a remnant grass layer and lacking a clear vertical structure, approximately 30% of woody saplings were colonizers, while in more developed large patches, with a structured tree layer, a well-defined shrub layer, and a herb layer consisting exclusively of forest species, colonizer plants occupied only 6% of the relative abundance of saplings. Therefore, a positive correlation between patch size and space occupancy by resident species was observed (Duarte et al. 2006b). In such a scenario, large-seeded colonizer plants were likely to have advantage over small-seeded species (e.g. Leishman 2001; Moles & Westoby 2006). Indeed, we found a significant positive association between patch size and mean seed diameter of colonizer species (Duarte et al. in press). However, we also found that phylogenetic and DAT determinants of seed size constrained that relationship, which was stronger when phylogeny and DAT influence on seed size was removed (see also Westoby et al. 1990; Kelly 1995). Thus, although the higher seed reserve content conferred advantage for plants establishing in large patches, colonization patterns seemed to be also influenced by processes related to attributes and/or behavior of dispersal agents. Understanding how the interplay between plant dispersal strategies and biological and ecological attributes of dispersers influence plant colonization is crucial to the comprehension of nucleation dynamics.

In this paper we examine the functional relevance of diaspore DAT as indicators of plant-disperser mutualisms in the colonization of *Araucaria* forest patches of different sizes by woody plant species. Firstly we evaluate the importance of dispersal by vertebrates on patch colonization by comparing three different patch size groups in terms of the proportion of vertebrate-dispersed plant species in relation to abiotically-dispersed species. Then we classify the vertebrate-dispersed diaspores into types defined by DAT, taking in consideration the influence of phylogenetic effects on diaspore attributes, and compare the occurrence of types in forest patches of different sizes. Lastly, we analyze the plant-frugivore network linking the colonizer species to fruit-consumer birds present in the study area in order to examine how diaspore types relate to number of interactions with fruit-consumer birds and to the frugivore attributes expressed at the plant-community level.

Material and Methods

Vegetation data

We analyzed a vegetation matrix describing 37 *Araucaria* forest patches scattered in a grassland site in south Brazilian highlands (29°28'S and 50°13'W, at ca. 900 m a.s.l.). After decades of cattle grazing and burning practices, the area has been released from human disturbances since 1994, allowing increasing regeneration in forest patches scattered in the grassland (Duarte et al. 2006b), and more biomass accumulation and woody plant establishment in the open field (Oliveira and Pillar 2004). Patches were previously divided into three groups according to area and structural development (Duarte et al. 2006b): *Nurse plants* ($N = 23$) were *Araucaria angustifolia* individuals isolated in the grassland (mean crown area ± standard error = 35 m^2 ± 5.2). *Small patches* ($N = 9$) were groups of forest woody plants with at least one adult tree and accompanying shrubs forming a continuous canopy, surrounded by a continuous herb layer (mean patch area ± standard error = 195.3 m^2 ± 37.9). Those patches lacked a clear vertical structure, and in general had few adult trees, mostly of *Myrcia retorta*, *Araucaria angustifolia*, *Myrcia guianensis* and *Myrsine lorentziana*, plus a variable amount of woody saplings. The canopies were considerably open, allowing grassland species to resist to some extent to forest development. *Large patches* (*N* = 5, data from Machado 2004) were sites with higher structural development when compared to nurse plants and small patches (mean patch area ± standard error = 1899.6 m^2 ± 255.7*)*. They had a structured tree layer, formed mainly by *Myrcia guianensis, Drimys brasiliensis, Myrcia retorta* and *Araucaria angustifolia,* a well-defined shrub layer, and a herb layer consisting exclusively of forest species. Duarte et al. (2006b) provide further details on the study area and data set.

Duarte et al. (2006b) compared those three patch groups by the relative abundance of woody saplings, and classified woody plants occurring in the patches as *colonizers*, i.e. those species occurring in the same patch size class only as saplings (individuals < 5 cm of diameter at breast height), or *resident*s, i.e. those species occurring as sapling and as assumed mature plants in the same patch size class (individuals > 5 cm of diameter at breast height). For this study, we transformed the abundance matrix generated by Duarte et al. (2006b) into a presence/absence matrix, defined a community matrix **C** of p =44 colonizer plant species (rows), belonging to 32 genera and 23 botanical families in the n forest patches (columns).

Phylogeny

We described taxonomically each colonizer species according to the phylogenetic classification of Angiosperms proposed by APG II (APG 2003). For this, we built a binary matrix **F**, defined by t taxonomic clades (rows), from higher monophyletic groups (like Magnoliids and Core Eudicots), to orders, families and genera, and p colonizer species (columns). We used matrix **F** to evaluate the phylogenetic determinants of DAT.

Diaspore dispersal mode and morphology

In each forest patch, we classified the dispersal mode of colonizer sapling diaspores into those 1) dispersed by vertebrates and 2) others, the latter including both abiotic and auto-dispersal (Tabarelli and Peres 2002). These later were excluded from the diaspore morphological analyses as described in the sequel.

Vertebrate-dispersed colonizer species were described by diaspore type, size and color (DAT). Detailed information on the preparation of the data matrix is available in Duarte et al. (In press), while the complete data matrix is presented in the Chapter 4 (Appendix 1). Berries and drupes represented 84% of diaspores, while the remaining 16% were arillate seeds (8%) or others (compound fruits, figs or pods, 8%). Most diaspores (ca. 68%) presented diameters smaller than ten millimeters, while only 5% had diaspores larger than 35 millimeters. Bright colors (black, violet, red, orange and white) were present in 87% of diaspores, while dull colors (green, brown and yellow) were present in the remaining 13% of colonizer diaspores. DAT information defined a binary matrix $\mathbf{D}$ describing $q = 15$ diaspore traits (rows) in $p = 38$ vertebrate-dispersed colonizer species (columns).

Plant-frugivore interactions

Data on plant-bird interactions were obtained from the available literature on bird diet and frugivory (see Appendix 1 at the end of this chapter). We used only information on plant-frugivore interactions for bird species found in the study area, according to a previous bird inventory (Fontana et al. unpubl.). Given the lack of available information, our interaction network was restricted to the plant genera level. We did not found any record of frugivory concerning the bird fauna of the study site for *Mollinedia* and *Xylosma*, and removed these genera from analyses. We defined a plant-frugivore network ($\mathbf{I}$) of $p = 24$ plant genera (rows) described by the presence/absence of interactions with s = 68 fruit consumer bird species (columns).

We characterized frugivores by body size, habitat use in time and space, and diet, since these traits might indicate functional affinities between diaspore types and frugivores. For this we used the available ornithological literature concerning those species occurring in the study area (Schubart et al. 1965; Morton 1977; Belton 1994; Hayes et al. 1994; Stotz et al. 1996; Sick 1997; Bencke & Kindel 1999; Fontana et al. 2003). Birds were categorized into three body size classes (small, medium and large). For this, we calculated the mean body mass (in g) ± 95% confidence interval ($\overline{\phi} \pm \mathrm{CI}_{95\%}$) for the bird species pool. Birds with mean body mass below $\overline{\phi} - \mathrm{CI}_{95\%}$ and above $\overline{\phi} + \mathrm{CI}_{95\%}$ were classified, respectively, as small and large, while those with diameter values within the $\overline{\phi} \pm \mathrm{CI}_{95\%}$ interval were classified as medium-sized. The use of grassland-forest mosaics by birds was evaluated both in temporal and spatial basis: *Habitat use in space*: birds were classified according to their occurrence in three habitat categories: open field, edge and forest. *Habitat use in time*: birds were classified into summer migrants or residents. The dietary preferences of birds were categorized into two main groups: Omnivorous-insectivorous and/or granivorous birds were considered as *non-frugivorous*, while omnivorous-frugivorous and specialist frugivores constituted the *frugivorous* group. The data defined a matrix **B** describing r = 10 bird traits (rows) in s = 68 bird species (columns).

Data analyses

We compared the proportion of vertebrate-dispersed species in the different patch size groups by ANOVA with randomization testing, and in the cases when significant differences were indicated, we also tested group contrasts by randomization (Pillar & Orlóci 1996; Manly 1997).

We were interested in evaluating which plant taxonomic level was more appropriate to define DAT-based diaspore types, i.e. the level in which the phylogenetic influence was weaker. For this, we analyzed the relationship between phylogeny (**F**) and DAT (**D**) at different taxonomic levels. Starting from the matrices **F** (phylogeny at species level) and **D** (DAT at species level) we obtained the respective matrices describing phylogeny and DAT variables at genus ($\mathbf{F}_G$, $\mathbf{D}_G$), family ($\mathbf{F}_F$, $\mathbf{D}_F$) and order ($\mathbf{F}_O$, $\mathbf{D}_O$) levels. For this, we computed the total occurrence of each DAT variable ($q = 15$) in each genus, family or order, and divided by the number of species in the respective taxonomic level. Thus, matrices $\mathbf{D}_G$, $\mathbf{D}_F$ and $\mathbf{D}_O$ contained the proportion of species presenting each diaspore trait. For each matrix pair, we computed Euclidean distances between sampling units (species, genera, families or orders) and evaluated the correlation between them using Mantel tests (Mantel 1967).

Starting from the lowest taxonomic level (species), we found the first non-significant correlation between phylogeny-DAT matrix pairs at the family level, which was then taken as more appropriate to define diaspore types (Table 1). Diaspore types were thus defined by a cluster analysis (WPGMA) of 19 botanical families, using Pearson correlations as similarity index. We evaluated the number of sharp groups using bootstrap resampling (Pillar 1999a). We then generated a matrix **T** describing v diaspore types (rows) in p vertebrate-dispersed colonizer species (columns). Since types were defined at family level, all species belonging to the same family were obligatorily grouped into the same diaspore type (which could contain more than one family). We compared the mean number of interactions of the different diaspore types with fruit-consumer birds by ANOVA with randomization testing (Manly 1997).

By multiplying matrix **T** by matrix $\mathbf{C}_\mathrm{V}$ containing p = 38 vertebrate-dispersed colonizer species in n= 36 patches (one was excluded from further analyses since it lacked vertebrate-dispersed species), we obtained a matrix **R**, describing n forest patches (columns) by v diaspore types (rows). Since species quantities were presence/absence values, **R** recorded the frequency of diaspore types in each forest patch. For scaling up bird traits and plant-bird interactions to the plant community level we defined by matrix multiplication $\mathbf{K} = \mathbf{BI}'$ describing p = 24 plant genera (columns) by the frequencies of r = 10 traits (rows) of the corresponding disperser birds. Then we defined a matrix $\mathbf{V} = \mathbf{KG}$, where **G** was derived from matrix $\mathbf{C}_\mathrm{V}$, and contained n forest patches (rows) described by p number of plant species per genus (columns). Matrix **V** contained the joint frequencies of plant genera and birds for each r bird trait (columns) in the n forest patches (rows). Matrix **V** was composed of sub-matrices corresponding to the four sets of complementary bird traits, that is, body size, habitat use in space and time, and dietary preferences. By concatenating matrices **V** and **R** we obtained a matrix **W** with r = 10 bird traits (matrix **V**) plus v = 4 diaspore types (matrix **R**) by n = 36 forest patches. Since the frequencies in **V** do not have the same nature as in **R**, the cells in the latter were adjusted in order to have in **R** the same row totals of each sub-matrix in **V**, that is, each b_{ij} cell in **R** was $b_{ij|ADJ} = b_{ij} v_{ki\cdot} / b_{i\cdot}$, where $b_{i\cdot}$ and $v_{ki\cdot}$ are the corresponding row totals in **R** and any sub-matrix in **V** respectively. Matrix **W** was then submitted to Correspondence Analysis (CA, Legendre & Legendre 1998). The stability of ordination axes was evaluated by bootstrapped auto-resampling (Pillar 1999b). Further, we evaluated the association between the scores of the first two CA axes and the log-transformed patch area using correlation analysis with randomization test (Pillar 2006). All analyses were performed using the software MULTIV v. 2.4 (Pillar 2006).

Results

From the 44 woody species colonizing *Araucaria* forest patches, 38 (86%) presented diaspores with attributes associated with dispersal by vertebrates. The proportion of vertebrate-dispersed species varied in the different patch size groups ($P < 0.01$). Beneath the crown of nurse plants, in average 95% of species presented vertebrate-dispersed diaspores. In small and large patches the proportion of vertebrate-dispersed species were lower than beneath nurse plants ($P < 0.05$), averaging 67% and 82%, respectively, and did not differ from each other ($P = 0.4$).

The WPGMA classification indicated the formation of four sharp groups of species defined by DAT variation at the family level (Table 1). The characteristics of diaspores in each group are summarized in the Table 2. Type A was formed by Fabaceae, Moraceae and Annonaceae (1 species per family), whose diaspores are characterized by medium to large pods (*Inga*), compound fruits (*Rollinia*) or figs (*Ficus*), yellow, brown or green colored. Diaspore type B was composed by 16 colonizer species of Thymelaeaceae (1 sp.), Winteraceae (1 sp.), Erythroxylaceae (1 sp.), Aquifoliaceae (3 spp.), Melastomataceae (4 spp.), Monimiaceae (1 sp.), Myrsinaceae (2 spp.), Rubiaceae (1 sp.), Lamiaceae (1 sp.) and Rutaceae (1 sp.). Type B diaspores were mostly characterized by small black or violet drupes or berries. Type C had 17 colonizer species of Myrtaceae (8 spp.), Lauraceae (6 spp.), Solanaceae (2 spp.) and Salicaceae (1 sp.). Type C diaspores were mostly small to large black, red or violet berries. Type D was formed by two species of Meliaceae (1 sp.) and Sapindaceae (1 sp.), with medium-sized, red, orange or white arillate seeds.

The plant-frugivore network showed a nested pattern, i.e. few plants were associated with many birds, and few birds were associated with many plants (Fig. 1a,b). Colonizer plant genera showed a variable number of interactions with consumer birds, ranging from one to 56 (Fig. 1a).

Nonetheless, the number of interactions per diaspore type did not differ among the different types (*P* = 0.89), and averaged 8.5 ± 5.2 (Mean ± CI_{95}).

The Correspondence Analysis (CA) of forest patches produced two stable axes (*P* = 0.01) representing ≅ 89% of the total variation in patches described by diaspore types and traits of the disperser birds of the colonizer plants (Fig. 2a). Type B diaspores were associated with nurse plants, while the other diaspore types were related to small and large patches (Fig. 2b). Furthermore, plant-frugivore interactions involving medium-sized birds, mostly frugivorous, associated with edge habitats and presenting a migrant habit were also associated with small and large patches, while those involving large-sized resident birds, mostly non-frugivorous and open field/forest inhabitants were associated to nurse plants (Fig. 2b). Interactions involving forest-inhabiting and resident birds were positively correlated with axis 2, while those involving edge-related and migrant birds were negatively correlated with the same axis 2 (Fig. 2b). Axis 1 was significantly correlated with patch area (*r* =0.66; *P* < 0.001, Fig. 2c), while axis 2 was not (*r* = 0.12; *P* > 0.5, Fig. 2c).

Discussion

The ecological relationship between plant diaspore traits and vertebrate disperser groups has been extensively demonstrated in the literature (Knight & Siegfried 1983; Gauthier-Hion et al. 1985; Wheelwright 1985; Tamboia et al. 1996; Rey et al. 1997; Bollen et al. 2004; Voigt et al. 2004). Morphological attributes of diaspores make them more appropriate for consumption by particular sets of frugivores in detriment of others. For instance, bird gape width limits the ingestion of diaspores above a compatible size (Wheelwright 1985, 1993; Rey et al. 1997; Lord 2004). Also, frugivorous birds discriminate fruits more suitable for consumption through their color (Wheelwright & Janson 1985; Mazer & Wheelwright 1993). Thus, although tight co-evolution involving plant-disperser species pairs is very unlikely to occur, given the intrinsically loose nature of plant-frugivore mutualisms (Jordano 1995; Herrera 2002), some relevant functional attributes of plants and dispersers can reveal meaningful interaction patterns, hardly detectable on a purely taxonomic basis (Zamora 2000). From a functional perspective, multiple sets of morpho-physiological variables related to dispersal (DAT, seed traits, reproductive effort, etc.) have been continuously submitted to natural selection. Therefore, phylogeny must not be viewed as a "noise" in present-day ecological patterns, but rather as a structuring agent underlying them (Westoby et al. 1995). By evaluating the taxonomic levels that maximized the independence of the clades in relation to DAT, we were able to detect the most suitable units for inter-specific comparisons involving colonizer plants, thus minimizing the variation inflation generated by eventual plesiomorphic traits, as well as the sub-estimation of apomorphic attributes of vertebrate-dispersed diaspores (Fischer & Chapman 1993).

The nested pattern showed by the plant-frugivore is a common trend observed in many plant-animal interaction networks (Bascompte et al. 2003). Nestedness is, expected to reflect varying levels of specialization among plant-animal species pairs (see also Lewinsohn et al. 2006). Nonetheless, in cases where interaction networks are formed by independent sets of plant and animals (as in the present case), nestedness can also be generated by the variation in abundance patterns of the species in the different locations (Wheelwright et al. 1984; Lewinsohn et al. 2006), which may lead to incomplete interaction networks, obviously biased to interactions involving the most abundant plants and/or frugivores. The functional approach adopted in this study apparently controlled this problem, since the DAT-defined diaspore types did not vary in terms of the number of interactions per type, i.e. all diaspore types had similar number of links with fruit-consumer birds (see also Zamora 2000). Interestingly, interactions involving type B diaspores (those associated with nurse plants), were proportionally more frequent among large resident birds, commonly non-frugivorous and inhabiting open areas. Thus, type B diaspores were associated with a wide range of fruit-consumer birds, both from a taxonomic and a functional perspective (body size, habitat use and diet), while other diaspore types showed interactions more restricted to typical frugivorous birds. Type B diaspores predominated among colonizer species occurring beneath the crowns of *Araucaria* nurse trees, suggesting that the colonization of these grass-dominated sites by bird-dispersed plants involved dispersal-generalist plants, i.e. species with functionally broad frugivory webs, while the colonization of larger patches was mainly promoted by dispersal-specialist plants whose frugivory webs depended on more typical frugivorous birds.

Some studies have suggested that the relationship between diaspore attributes associated with offspring dispersal strategies (namely seed size/number trade-off) and colonization success might be determined, at least partially, by diaspore transport/deposition patterns into new colonization sites by dispersers (Westoby et al. 1990; Kelly 1995). Analyzing the variation pattern in seed size/seed number of woody plants colonizing *Araucaria* forest patches, we observed (Duarte et al. in press) that in larger patches, colonizer plants with more seed reserves had some advantage over small-seeded species; however the positive association between seed size and patch area was greatly improved when we removed the joint effect of phylogeny and DAT over seed size, suggesting that different selective forces were acting during patch colonization. In the present study, diaspore types related to larger patches (A, C and D) were mostly associated with medium frugivorous birds, whose frugivory patterns are probably constrained by diaspore attributes, like size (Wheelwright 1985; Mazer & Wheelwright 1993; Rey et al. 1997; Lord 2004). Since in our study site diaspore and seed sizes of colonizer species were positively correlated traits (Duarte et al. in press, Electronic Appendix, http:// coming soon!), we might hypothesize a trade-off involving the amount of reserves contained in the seed and the probability of the diaspore being transported by a frugivore. That is to say, if from a plant perspective a larger seed represent more reserves for the offspring, which is especially important under closed canopies, then from the disperser perspective diaspore size might limit its handling by the frugivore, preventing its further dispersal.

Our results indicated that plant colonization in *Araucaria* forest patches developing into natural grasslands and recovering from man-made disturbances relied mostly on vertebrate seed dispersers. We finalize this paper highlighting that the nucleation of forest into open areas is a process related to species (plants and animals) that are very abundant in forest-grassland ecotones and have very low appeal for conservationists. Nowadays, those common and unappealing species have been severely threatened, since the current target of human-made degradation in *Araucaria* forest-*Campos* grassland in south Brazilian highlands is the natural grassland, which can sustain a very rich biota, and from whose conservation relies many ecological processes related to the structure and dynamics of the *Araucaria* forests. Only by conserving processes (instead of single species) we can guarantee the long-term maintenance of the forests with *Araucaria angustifolia*.

Aknowledgements

The authors thank botanists Dr. Maria Leonor D’El Rei Souza (UFSC) and Manuela Boleman Wiesbauer, who kindly provided information about some plant diaspores, the biologist MSc. Rafael E. Machado for kindly providing us data on the presence of species in large forest patches, Gisele C. Pinheiro for the revision of the bird traits, and Andreas Kindel and Nathaniel T. Wheelwright for valuable suggestions on earlier versions of this paper. This study had logistic support from CPCN Pró-Mata PUCRS and was funded by research grants and fellowships from CAPES (project 005/02) and CNPq (projects 500686/2003-3 and 141810/2003-3) to V. Pillar and L. da S. Duarte. Part of this work was carried out with the aid of a grant from the Inter-American Institute for Global Change Research (IAI) CRN-2005 which is supported by the US National Science Foundation (Grant GEO-0452325).

References

Anon. 2007. *IPNI - The International Plant Names Index.* URL: http://www.ipni.org [accessed from January to March 2007].

APG 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399-436.

Bascompte, J., Jordano, P., Melián, C.J. & Olesen, J.M. 2003. The nested assembly of plant-animal mutualistic networks. *Proc. Nat. Acad. Sci.* 100: 9383-9387.

Behling, H. 2002. South and southeast Brazilian grasslands during Late Quaternary times: a synthesis. *Palaeogeo. Palaeoclim. Palaeoecol.* 177: 19-27.

Behling, H. & Pillar, V.D. 2007. Late Quaternary vegetation, biodiversity and fire dynamics on the southern Brazilian highland and their implication for conservation and management of modern Araucaria forest and grassland ecosystems. *Phil. Trans. Royal Soc. London Biol. Sci.* 362: 243-251.

Belton, W. 1994. *Aves do Rio Grande do Sul, distribuição e biologia*. Ed. Unisinos, São Leopoldo, Brazil.

Bencke, G.A. & Kindel, A. 1999. Bird counts along an altitudinal gradient of Atlantic forest in northeastern Rio Grande do Sul, Brazil. *Rev. Bras. Ornitol.* 7: 91-107.

Bollen, A., Elsacker, L.V. & Ganzhorn, J.U. 2004. Tree dispersal strategies in the littoral forest of Sainte Luce (SE-Madagascar). *Oecologia* 139: 604–616.

Bond, W.J. & Midgley, G.F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biol.* 6: 865-869.

Bond, W.J., Midgley, G.F. & Woodward, F.I. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biol.* 9: 973-982.

Bruno J.F., Stachowicz J.J. & Bertness M.D. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18: 119-125.

Callaway, R.M. 1995. Positive interactions among plants. *Bot. Rev.* 61: 306-349.

CBRO 2006. *Lista de Aves do Brasil.* Available at www.cbro.org.br. Accessed in March 2007.

Dennis, A.J. & Westcott, D.A. 2006. Reducing complexity when studying seed dispersal at community scales: a functional classification of vertebrate seed dispersers in tropical forests. *Oecologia* 149: 620-634.

Duarte, L.S., Dos Santos, M.M.G., Hartz, S.M. & Pillar, V.D. 2006a. Role of nurse plants on *Araucaria* Forest expansion over grassland in south Brazil. *Aust. Ecol.* 31:520-528.

Duarte, L.S., Machado, R.E., Hartz, S.M. & Pillar, V.D. 2006b. What saplings can tell us about forest expansion over natural grasslands. *J. Veg. Sci.* 17: 799-808.

Duarte, L.S., Carlucci, M.B., Hartz, S.M. & Pillar, V.D. In press. Plant dispersal strategies and the colonization of *Araucaria* forest patches in a grassland-forest mosaic. *J. Veg. Sci.*

Fischer, K.E. & Chapman, C.A. 1993. Frugivores and fruit syndromes: differences in patterns at the genus and species level. *Oikos* 66: 472-482.

Fontana, C.S., Bencke, G.A. & Reis, R.E. 2003. *Livro Vermelho da Fauna Ameaçada de Extinção no Rio Grande do Sul.* Edipucrs, Porto Alegre, Brazil.

Galindo-González, J., Guevara, S. & Sosa, V.J. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conserv. Biol.* 14: 1693-1703.

Gauthier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C., Thiollay, J.M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65: 324-337.

Guevara, S., Meave, J., Moreno-Casasola, P. & Laborde, J. 1992. Floristic composition and structure of vegetation under isolated trees in neotropical pastures. *J. Veg. Sci.* 3: 655-664.

Hayes, F.E., Scharf, P.A. & Ridgely, R.S. 1994. Austral bird migrants in Paraguay. *Condor* 96: 83-97.

Herrera, C.M. 2002. Seed dispersal by vertebrates. In: Herrera, C.M. & Pellmyr, O. (eds.) *Plant-Animal Interactions – An Evolutionary Approach*. p. 185-208. Blackwell Publishing, Malden, USA.

Holl, K.D. 2002. Effect of shrubs on tree seedling establishment in an abandoned tropical pasture. *J. Ecol.* 90: 179-187.

Howe, H.F. & Smallwood, J. 1982. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201-228.

Janson, C.H. 1983. Adaptation of fruit morphology to dispersal agents in a Neotropical Forest. *Science* 219: 187-189.

Jordano, P. 1995. Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant-animal interactions. *Am. Nat.* 145: 163-191.

Jordano, P., Garcia, C., Godoy, J.A. & García-Castaño, J.L. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proc Nat Acad Sci USA* 104: 3278-3282.

Kelly, C.K. 1995. Seed size in tropical trees: a comparative study of factors affecting seed size in Peruvian angiosperms. *Oecologia* 102: 377-388.

Klein, R.M. 1960. O aspecto dinâmico do pinheiro brasileiro. *Sellowia* 12: 17-51.

Knight, R.S. & Siegfried, W.R. 1983. Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. *Oecologia* 56: 405-412.

Legendre, P. & Legendre, L. 1998. *Numerical Ecology*, 2nd edn. Elsevier, Amsterdam, The Netherlands.

Leishman, M. 2001. Does the seed size/number trade-off model determine plant community structure? An assessment of the model mechanisms and their generality. *Oikos* 93: 294-302.

Lewinsohn, T.M., Prado, P.I., Jordano, P., Bascompte, J. & Olesen, J.M. 2006. Structure in plant animal interaction assemblages. *Oikos* 113: 174-184.

Lord, J.M. 2004. Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. *Aust. Ecol.* 29: 430–436.

Machado, R.E. 2004. *Padrões Vegetacionais em Capões de Floresta com Araucaria no Planalto Nordeste do Rio Grande do Sul, Brasil*. MSc. Thesis, UFRGS, Porto Alegre, Brazil.

Manly, B.F.J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*, 2nd ed. Chapman and Hall, London, UK.

Mantel, N. 1967. The detection of disease clustering and a generalized regression approach. *Canc. Res.* 27: 209-220.

Mazer, S.J. & Wheelwright, N.T. 1993. Fruit size and shape: allometry at different taxonomic levels in bird-dispersed plants. *Evol. Ecol.* 7: 556-575.

McClanahan, T.R. & Wolfe. R.W. 1993. Accelerating forest succession in a fragmented landscape: the role of birds and perches. *Conserv. Biol.* 7: 279-288.

Moles, A. & Westoby, M. 2006. Seed size and plant strategy across the whole life cycle. *Oikos* 113:91-105.

Morton, S.E. 1977. Intratropical migration in the yellow-green vireo and piratic flycatcher.*The Auk* 94: 97-106.

Nathan, R. & Muller-Landau, H.C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol. Evol.* 15: 278-285.

Oliveira J.M. & Pillar, V.D. 2004. Vegetation dynamics on mosaics of *Campos* and Araucaria forest between 1974 and 1999 in Southern Brazil. *Commun. Ecol.* 5: 197-202.

Pillar, V.D. 1999a. How sharp are classifications? *Ecology* 80: 2508-2516.

Pillar, V.D. 1999b. The bootstrapped ordination re-examined. *J. Veg. Sci.* 10: 895-902.

Pillar, V.D. 2006. *MULTIV; Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling; User's Guide v. 2.4.* Departamento de Ecologia, UFRGS, Porto Alegre, Brazil (software and manual available from http://ecoqua.ecologia.ufrgs.br).

Pillar, V.D. & Orlóci, L. 1996. On randomization testing in vegetation science: multifactor comparisons of relevé groups. *J. Veg. Sci.* 7: 585-592.

Rambo, B. 1994. *A Fisionomia do Rio Grande do Sul*, 3rd ed. Ed Unisinos, São Leopoldo, Brazil.

Rey, P.J., Gutiérrez, J.E., Alcántaram, J. & Valera, F. 1997. Fruit size in wild olives: implications for avian seed dispersal. *Func. Ecol.* 11: 611-618.

Ridley, H.N. 1930. *The Dispersal of Plants Throughout the World.* L Reeve and Co, Kent, UK.

Russo, S.E., Portnoy, S. & Augspurger, C.K. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* 87: 3160–3174.

Scholes, R.J. & Archer, S.R. 1997. Tree-grass interactions in savannas. *Ann. Rev. Ecol. Syst.* 28: 517-544.

Schubart,O., Aguirre, A.C. & Sick, H. 1965. Contribuição para o conhecimento da alimentação das aves brasileiras. *Arquiv. Zool.* 12: 95-249.

Sick, H. 1997. *Ornitologia Brasileira*. Ed. Nova Fronteira, Rio de Janeiro, Brazil.

Shiels, A.B. & Walker, L.R. 2003. Bird perches increase forest seeds on Puerto Rican landslides. *Restor. Ecol.* 11: 457-465.

Slocum, M.G. & Horwitz, C.C. 2000. Seed arrival under different genera of trees in a neotropical pasture. *Plant Ecol.* 149: 51-62.

Snow, D.W. 1981. Tropical frugivorous birds and their food plants: a world survey. *Biotropica* 13: 1-14.

Stotz, D.F., Fitzpatrick, J., Parker III, T.A. & Moskovits, D.K. 1996. *Neotropical Birds: Ecology and Conservation.* University of Chicago Press, Chicago, USA.

Tamboia, T., Cipollini. M.L. & Levey, D.J. 1996. An evaluation of vertebrate seed dispersal syndromes in four species of black nightshade (*Solanum* sect. *Solanum*). *Oecologia* 107: 522-532.

Tabarelli, M. & Peres, C.A. 2002. Abiotic and vertebrate seed dispersal in the Brazilian Atlantic Forest: implications for forest regeneration. *Biol. Conserv.* 106: 165-176.

Toh, I., Gillespie, M. & Lamb, D. 1999. The role of isolated trees in facilitating tree seedling recruitment at a degraded sub-tropical rainforest site. *Restor. Ecol.* 7:288-297.

Van der Pijl, L. 1982. *Principles of Dispersal in Higher Plants.* Springer-Verlag, Berlin, Germany.

Voigt, F.A., Bleher, B., Fietz, J., Ganzhorn, J.U., Schwab, D. & Böhning-Gaese, K. 2004. A comparison of morphological and chemical fruit traits between two sites with different frugivore assemblages. *Oecologia* 141: 94-104.

Westoby, M, Leishman, M.R. & Lord, J.M. 1995. On misinterpreting the ‘phylogenetic correction’. *J. Ecol.* 83: 53-534.

Westoby, M.; Rice, B. & Howell, J. 1990. Seed size and plant growth as factors in dispersal spectra. *Ecology* 71: 1307-1315.

Wheelwright, N.T. 1985. Fruit size, gape width and the diets of fruit-eating birds. *Ecology* 66: 808-818.

Wheelwright, N.T. 1993. Fruit size in a tropical tree species: variation, preference by birds, and heritability. In Fleming, T.H. & Estrada, A. (eds.). *Frugivory and Seed Dispersal: Ecological and Evolutionary Aspects.* p. 163-174. Kluwer Academic Publishers, Belgium.

Wheelwright, N.T., Haber, W.A., Murray, K.G. & Guindon, C. 1984. Tropical fruit-eating birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16: 173-192.

Wheelwright, N.T. & Janson, C.H. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. *Am. Nat.* 126: 777-799.

Wunderle Jr., J.M. 1997. The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *For. Ecol. Managem.* 99: 223-235.

Yarranton, G.A. & Morrison, R.G. 1974. Spatial dynamics of a primary succession: nucleation. *J. Ecol.* 62: 417-428.

Zamora, R. 2000. Functional equivalence in plant-animal interactions: ecological and evolutionary consequences. *Oikos* 88: 442-447.

Table 1. Relationship between phylogenetic affinities among woody plants colonizing *Araucaria* forest patches and their diaspore traits related to disperser attraction (DAT). N_i is the number of sampling units in the original data matrix. r_M: Mantel correlation coefficient (*: $P < 0.001$; **: $P < 0.03$; NS: $P > 0.3$). Diaspore types were obtained by WPGMA classification. The number of sharp groups was defined by P values > 0.1, obtained by bootstrapped auto-resampling.

Taxonomic level	N_i	r_M	Number of sharp groups	$P_{Gnull \leq Gcalc}$
Species	38	0.32 *	0	0.09
Genus	26	0.19 **	4	0.15
Family	19	≅ 0.00 NS	4	0.14
Order	14	-0.10 NS	5	0.13

Table 2. Diaspore types defined by attributes related to disperser attraction (DAT) at the family level. *N*: Number of species contained in the respective diaspore type. Values among parentheses indicate the proportion of the variable state in the diaspore type.

Diaspore type	*N*	DAT		
		Morphology	Size	Colour
A	3	Compound fruits, pods or figs	Large (67%) or Medium (33%)	Yellow (50%), brown (25%) or green (25%)
B	16	Drupes (63%), berries (31%) or arillate seeds (6%)	Small (81%), Medium (13%) or Large (6%)	Black (48%), violet (26%), red (15%), orange (7%) or yellow (4%)
C	17	Berries	Medium (53%), Small (24%), or Large (24%)	Black (42%), red (27%), violet (12%), orange (8%), yellow (8%) or brown (4%)
D	2	Arillate seeds	Medium	Red (33%), orange (33%) or white (33%)

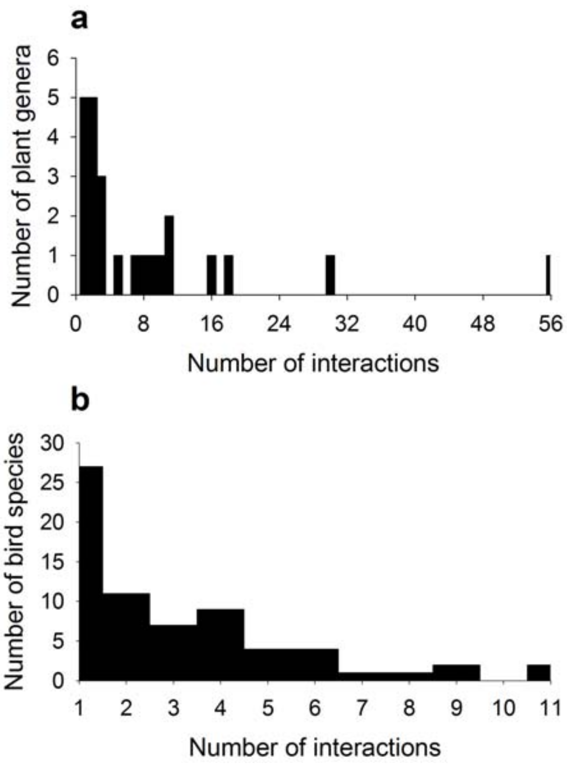

Fig. 1. *Distribution pattern of plant-frugivore interactions among (a) colonizer plants and (b) birds.*

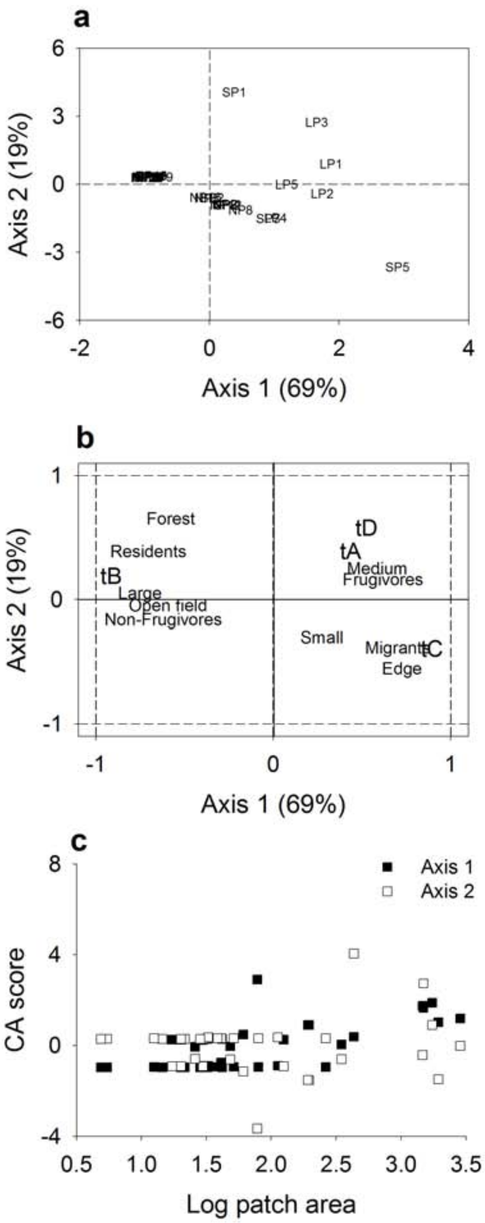

Fig. 2. *Correspondence Analysis (CA) of diaspore type frequencies in forest patches at different structural development stages in natural grassland in southern Brazil. a) CA scatter diagram of patches. NP: nurse plants, SP: small patches, LP: large patches. Axes 1 and 2 were significantly stable (*$\mathrm{P} < 0.01$*). b) Projection of diaspore types (tA to tD) and bird traits on CA axes 1 and 2. All diaspore types and bird traits were significantly correlated with axis 1 (*$\mathrm{P} < 0.02$*), except ´Small´ (*$\mathrm{P} = 0.11$*). tA, tC and tD were significantly correlated with CA axis 2 (*$\mathrm{P} \leq 0.05$*). Bird*

traits correlated with CA axis 2 ($P < 0.08$*) - Body size: ‘Small’; Habitat use in space: ´Edge´, ´Forest. Habitat use in time: ‘Migrants’, ‘Residents’. c) Relationship between patch area and ordination scores (Axis 1:* $r = 0.66$*;* $P < 0.001$*. Axis 2:* $r = 0.12$*;* $P > 0.5$*).*

Appendix 1.

Plant-frugivore network for woody plants colonizing *Araucaria* forest patches in a forest-grassland southern Brazil.

Bird species	Plant genus[1]																							
	Ca	*Cl*	*Da*	*Dr*	*Er*	*Eu*	*Fi*	*Il*	*In*	*Le*	*Ma*	*Mi*	*My*	*Mc*	*Ms*	*Ne*	*Oc*	*Ps*	*Ro*	*Ru*	*Si*	*So*	*Vi*	*Za*
CARDINALIDAE																								
Saltator maxillosus															X							X		
Saltator similis												X		X	X	X				X		X		
COLUMBIDAE																								
Geotrygon montana															X									
Leptotila rufaxilla												X		X	X									
Leptotila verreauxi															X									
CONOPOPHAGIDAE																								
Conopophaga lineata															X									
CORVIDAE																								
Cyanocorax caeruleus						X	X								X							X		
COTINGIDAE																								
Carpornis cucullatus			X			X	X			X		X		X	X	X	X			X	X			
Procnias nudicollis							X				X			X		X								
EMBEREZIDAE																								
Embernagra platensis															X									
Haplospiza unicolor															X									
Poospiza thoracica										X														
Zonotrichia capensis							X								X									
FRINGILLIDAE																								
Chlorophonia cyanea															X									
Euphonia chalybea															X				X					
Euphonia pectoralis															X									
ICTERIDAE																								
Cacicus chrysopterus	X														X									

Appendix 1. Cont.

Bird species	Plant genus[1]																						
	Ca	*Cl*	*Da*	*Dr*	*Er*	*Eu*	*Fi*	*Il*	*In*	*Le*	*Ma*	*Mi*	*My*	*Mc*	*Ms*	*Ne*	*Oc*	*Ps*	*Ro*	*Ru*	*Si*	*So*	*Vi*	*Za*
MIMIDAE																								
Mimus saturninus												X			X		X							
ODONTOPHORIDAE																								
Odontophorus capueira															X									
PARULIDAE																								
Basileuterus culicivorus												X												
Parula pitiayumi												X												
PICIDAE																								
Colaptes campestris												X												
Colaptes melanochlorus															X									
PIPRIDAE																								
Chiroxiphia caudata	X						X	X				X		X	X	X	X							
Piprites pileata															X									
PSITTACIDAE																								
Pionopsitta pileata															X							X		
Pionus maximiliani						X	X		X						X									
Pyrrhura frontalis							X		X			X		X	X	X	X	X				X		
Triclaria malachitacea						X							X					X						
RAMPHASTIDAE																								
Ramphastus dicolorus	X					X	X					X			X								X	
THAMNOPHILIDAE																								
Dysithamnus mentalis															X									
Thamnophilus caerulescens															X									
Thamnophilus ruficapillus															X									

Appendix 1. Cont.

Bird species	Plant genus[1]																						
	Ca	*Cl*	*Da*	*Dr*	*Er*	*Eu*	*Fi*	*Il*	*In*	*Le*	*Ma*	*Mi*	*My*	*Mc*	*Ms*	*Ne*	*Oc*	*Ps*	*Ro*	*Ru*	*Si*	*So*	*Vi*	*Za*
THRAUPIDAE																								
Dacnis cayana	X											X		X										X
Pipraeidea melanonota										X														
Pyrrhocoma ruficeps															X									
Stephanophorus diadematus		X		X	X			X		X		X		X	X			X		X		X		
Tachyphonus coronatus							X			X		X		X	X									
Tangara preciosa				X			X							X		X								
Thraupis cyanoptera												X						X	X					
Thraupis sayaca		X				X	X					X		X	X			X				X	X	
Trichothraupis melanops										X		X					X							
TINAMIDAE																								
Crypturellus obsoletus															X									
TITYRIDAE																								
Pachyramphus castaneus															X									
Pachyramphus polychopterus															X	X								
Pachyramphus validus												X			X									
Schiffornis virescens															X									
TITYRIDAE																								
Tityra cayana															X	X	X							
TROGONIDAE																								
Trogon rufus															X									
Trogon surrucura															X	X								
TURDIDAE																								
Platycichla flavipes	X					X	X					X			X									
Turdus albicollis										X		X			X	X								
Turdus amaurochalinus							X					X			X	X	X							
Turdus rufiventris						X	X					X			X	X	X							
Turdus subalaris															X									

Appendix 1. Cont.

Bird species	Plant genus[1]																							
	Ca	*Cl*	*Da*	*Dr*	*Er*	*Eu*	*Fi*	*Il*	*In*	*Le*	*Ma*	*Mi*	*My*	*Mc*	*Ms*	*Ne*	*Oc*	*Ps*	*Ro*	*Ru*	*Si*	*So*	*Vi*	*Za*
TYRANNIDAE																								
Attila phoenicurus															X									
Camptostoma obsoletum												X			X									
Elaenia mesoleuca				X						X		X			X									
Empidonomus varius												X			X	X	X							
Mionectes rufiventris	X											X			X	X								
Muscipipra vetula															X									
Myiarchus swansonii												X			X	X								
Myiodinastes maculatus	X						X					X			X	X	X							
Phylloscartes difficilis															X									
Tolmomyias sulphurescens												X			X									
Tyrannus melancholicus	X						X			X		X			X	X	X							
VIREONIDAE																								
Cyclarhis gujanensis	X																							X
Vireo olivaceus	X											X			X	X								X

[1] *Ca*: *Cabralea*; *Cl*: *Calyptranthes*; *Da*: *Daphnopsis*; *Dr*: *Drimys*; *Er*: *Erythroxylum*; *Eu*: *Eugenia*; *Fi*: *Ficus*; *Il*: *Ilex*; *In*: *Inga*; *Le*: *Leandra*; *Ma*: *Matayba*; *Mi*: *Miconia*; *My*: *Myrceugenia*; *Mc*: *Myrcia*; *Ms*: *Myrsine*; *Ne*: *Nectandra*; *Oc*: *Ocotea*; *Ps*: *Psidium*; *Ro*: *Rollinia*; *Ru*: *Rudgea*; *Si*: *Siphoneugena*; *So*: *Solanum*; *Vi*: *Vitex*; *Za*: *Zanthoxylum.*

References

Cáceres, N.C. & Moura, M.O. 2003. Fruit removal of a wild tomato, *Solanum granulosoleprosum* Dunal (Solanaceae), by birds, bats and non-flying mammals in an urban Brazilian environment. *Rev. Bras. Zool.* 20: 519-522.

Fadini, R.F. & De Marco Jr., P. 2004. Interações entre aves frugívoras e plantas em um fragmento de mata atlântica de Minas Gerais. *Ararajuba* 12: 97-103.

Francisco, M.R., Galetti, M. 2001. Frugivoria e dispersão de sementes de *Rapanea lancifolia* (Myrsinaceae) por aves numa área de Cerrado no estado de São Paulo. *Ararajuba* 9: 13-19

Francisco, M.R., Galetti, M. 2002. Aves como potenciais dispersoras de sementes de *Ocotea pulchella* Mart (Lauraceae) numa área de vegetação de Cerrado no sudeste brasileiro. *Rev. Bras. Bot.* 25: 11-17.

Galetti, M. 1997. Seasonal abundance and feeding ecology of parrots and parakeets in a lowland Atlantic forest in Brazil. *Ararajuba* 5: 115-126.

Galetti, M. & Pizo, M.A. 1996. Fruit eating by birds in a forest fragment in southeastern Brazil. *Ararajuba* 4: 71-79.

Galetti, M., Laps, R., Pizo, M.A. 2000. Frugivory by toucans (Ramphastidae) at two altitudes in the Atlantic Forest of Brazil. *Biotropica* 32: 842-850.

Galetti, M. & Stotz, D. 1996. *Miconia hypoleuca* (Melastomataceae) como espécie-chave para aves frugívoras no sudeste do Brasil. *Rev. Bras. Biol.* 56: 435-439.

Hasui, E. & Höfling, E. 1998. Preferência alimentar das aves frugívoras de um fragmento de floresta estacional semidecídua secundária, São Paulo, Brasil. *Iheringia (Ser. Zool.)* 84: 43-64.

Kindel, A. 1996. *Interações entre plantas ornitocóricas e aves frugívoras na Estação Ecológica de Aracuri, Muitos Capões, RS*. MSc Thesis, UFRGS, Porto Alegre, Brazil.

Krügel, M.M., Burger, M.I., Alves, M.A. 2006. Frugivoria por aves em *Nectandra megapotamica* (Lauraceae) em uma área de Floresta Estacional Decidual no Rio Grande do Sul, Brasil. *Iheringia (Ser. Zool.)* 96: 17-24.

Manhães, M.A. 2003. Dieta de traupíneos (Passeriformes, Emberezidae) no Parque Estadual do Ibitipoca, Minas Gerais, Brasil. *Iheringia (Ser. Zool.)* 93: 59-73.

Manhães, M.A., Assis, L.C.S. & Castro, R.M. 2003. Frugivoria e dispersão de sementes de Miconia urophylla (Melastomataceae) por aves em um fragmento de Mata Atlântica secundária em Juiz de Fora, Minas Gerais, Brasil. *Ararajuba* 11: 173-180.

Mendonça-Lima, A. & Fontana, C.S. 2000. Composição, freqüência e aspectos biológicos da avifauna no Porto Alegre Country Clube, Rio Grande do Sul. *Ararajuba* 8: 1-8.

Marcondes-Machado, L.O. 2002. Comportamento alimentar de aves em *Miconia rubiginosa* (Melastomataceae) em fragmento de Cerrado, São Paulo. *Iheringia (Ser. Zool.)* 92: 97-100.

Mendonça-Lima, A., Fontana, C.S. & Mähler, Jr., J.K.F. 2001. Itens alimentares consumidos por aves no nordeste do Rio Grande do Sul, Brasil. *Tangara* 1:115-124.

Pineschi, R.B. 1990. Aves como dispersores de sete espécies de Rapanea (Myrsinaceae) no maciço do Itatiaia, estados do Rio de Janeiro e Minas Gerais. *Ararajuba* 1: 73-78.

Pizo, M.A. 1996. Feeding ecology of two *Cacicus* species. *Ararajuba* 4: 87-92.

Pizo, M.A. 1997. Seed dispersal and predation in two populations of *Cabralea canjerana* (Meliaceae) in the Atlantic forest of southeastern Brazil. *J. Trop. Ecol.* 13: 559-578.

Pizo, M.A., Silva, W.R., Galetti, M. & Laps, R. 2003. Frugivory in cotingas of the Atlantic Forest of southeast Brazil. *Ararajuba* 10: 177-185.

Pizo, M.A., Simão, I. & Galetti, M. 1995. Diet and flock size of sympatric parrots in the Atlantic Forest of Brazil. *Ornitol. Neotrop.* 6: 87-95.

Ragusa-Netto, J. 2002. Fruiting phenology and consumption by birds in *Ficus calyptroceras* (Miq.) Miq. (Moraceae). *Braz. J. Biol.* 62: 339-346.

Reinert, B.L. & Bornschein, M.R. 1998. Alimentação da gralha-azul (*Cyanocorax caeruleus*, Corvidae). *Ornitol. Neotrop.* 9:213-217.

Rodrigues, M. 1995. Spatial distribution and food utilization among tanagers in southeastern Brazil (Passeriformes: Emberezidae). *Ararajuba* 3: 27-32.

Simão, I., Santos, F.A.M. & Pizo, M.A. 1997. Vertical stratification and diet of psittacids in a Tropical lowland forest of Brazil. *Ararajuba* 5: 169-174.

Capítulo 6. Conclusões

Ampliando o modelo de Klein

Do ponto de vista da Ciência da Vegetação, o modelo de Klein é teoricamente sólido, visto que grande parte do corpo teórico voltado ao entendimento de padrões, processos e mecanismos que explicam a estrutura e a dinâmica de comunidades baseia-se na premissa (geralmente implícita) de que variações climáticas e edáficas determinam as mudanças observadas na vegetação, que por sua vez determinam a dinâmica nos demais níveis tróficos. Interessantemente, tanto a escola organicista de Clements e seguidores (Clements 1928, Tansley 1949, Daubenmire 1968), quanto a escola individualista de Gleason e seguidores (Gleason 1939, Glenn-Lewin et al. 1992), baseiam suas visões neste mesmo pressuposto.

No modelo de Klein, indivíduos de *Araucaria angustifolia* isolados em áreas campestres são agentes nucleadores de manchas florestais, notadamente em sítios com pouca disponibilidade hídrica (xerossere, Klein 1960). Além disso, o modelo propõe que mudanças estruturais (maior sombreamento do estrato inferior) geradas pelo desenvolvimento das manchas florestais levam à substituição das espécies vegetais nelas presentes, em função dos diferentes níveis de tolerância das espécies ao sobreamento crescente. Durante a execução dos diferentes estudos que compõe esta tese, grande parte dos resultados ratificaram quantitativamente o modelo observacional desenvolvido há quase 50 anos por Roberto Klein. No Capítulo 2 foi demonstrada a importância da *Araucaria* como planta-berçário para espécies florestais. Os Capítulos 3 e 4 mostraram os efeitos da variação estrutural nas manchas florestais sobre as assembléias de plantas lenhosas residentes e colonizadoras, tanto sob o ponto de vista estrutural (composição, riqueza e diversidade, Cap. 3), quanto sob o ponto de vista de estratégias adaptativas relacionadas à colonização de ambientes estruturalmente diferenciados (Cap. 4). Certamente o modelo de Klein (1960) de dinâmica vegetacional da floresta com *Araucaria* permanece atual, sofisticado e fonte de diversas perguntas a serem respondidas por ecólogos do presente e do futuro.

Por outro lado, o modelo de Klein em particular e os modelos de dinâmica de comunidades em geral, negligenciam a importância de outros níveis tróficos nos processos dinâmicos em comunidades. Neste sentido, o presente estudo amplia o modelo original de Klein, pois inclui um fator decisivo no processo de colonização de áreas abertas por espécies florestais, ou seja, a fauna dispersora de diásporos, responsável pelo transporte da maior parte das sementes das florestas com *Araucaria* para os campos. Segundo Daubenmire (1968), a importância da fauna na dinâmica das comunidades residiria principalmente nas fases iniciais de desenvolvimento destas, através do transporte de diásporos vegetais (frutos e sementes), polinização e alteração do ambiente (esta última atividade estreitamente relacionada à atividade humana). Posteriormente, os processos autogênicos e alogênicos de desenvolvimento da comunidade, relacionados às mudanças sucessionais, seriam determinados pela vegetação.

Mas será a fauna simplesmente uma conseqüência da vegetação? Nos Capítulos 4 e 5 desta tese observamos que plantas colonizadoras de manchas de floresta com *Araucaria* são dispersas predominantemente por vertebrados, e apresentam diásporos com adaptações tanto relacionadas à dispersão e sobrevivência da prole, quanto à atração de agentes dispersores. Por sua vez, atributos morfológicos, fisiológicos e ecológicos da fauna presente nas manchas florestais geram padrões de interação mutualística com as plantas colonizadoras, os quais variam em função da estrutura das manchas. Certamente mudanças estruturais na vegetação produzem habitats diferenciados para distintos grupos animais. Porém, dificilmente estes últimos possam ser considerados agentes passivos nos processos ecológicos que promovem mudanças na comunidade. Modelos realísticos de dinâmica de comunidades devem incluir interações multitróficas como fatores determinantes no processo. Por extensão, modelos de nucleação de manchas florestais nos campos do Planalto Sul-brasileiro devem incluir necessariamente variáveis relacionadas ao processo de dispersão de diásporos das áreas florestais contínuas para áreas abertas, dentre as quais os tipos de agentes dispersores, tanto do ponto de vista taxonômico (aves, mamíferos), quanto funcional (uso do habitat, dieta principal, morfometria, etc.).

De que forma a fauna dispersora pode determinar direções sucessionais em manchas florestais? Sob o ponto de vista das plantas, o processo de dispersão envolve dois fatores fundamentais e conflitantes: transporte de diásporos e estabelecimento da prole no novo habitat. Este "dilema" tem sido exaustivamente discutido na literatura, e foi amplamente discutido no Capítulo 4 desta tese. O ponto fundamental é que o sucesso das estratégias de dispersão das plantas é uma função do habitat a ser colonizado. No modelo de Klein, as plantas que colonizam manchas mais desenvolvidas devem ser mais tolerantes ao sombreamento do que as primeiras colonizadoras. Em termos de estratégia de dispersão, a tolerância ao sombreamento será uma função da quantidade de reservas das sementes. Logo, espécies colonizadoras de fases avançadas de desenvolvimento das manchas deverão ter sementes maiores. Porém, para que estas espécies alcancem o novo habitat, deverão ser transportadas por agentes dispersores proporcionalmente grandes, e que sejam atraídos de alguma forma pelo habitat. Conseqüentemente, a ausência destes dispersores poderá alterar a dinâmica de nucleação das manchas (ver Silva & Tabarelli 2000). Quando incluímos este simples fator no modelo de Klein, vemos que o processo torna-se muito mais complexo e interdependente do que no modelo original (Fig. 1a). O *pool* de espécies colonizadoras (*c*) que chega até as manchas será uma função do uso das mesmas por um dado grupo de agentes dispersores (*d*). Quanto mais estruturalmente desenvolvidas forem as manchas, maior será o sombreamento. Além disso, em manchas mais desenvolvidas há o recrutamento local de novos indivíduos por plantas adultas residentes, diminuindo o espaço para o estabelecimento de novas espécies. Portanto, quanto maiores forem as sementes das espécies em *c* maiores serão suas chances de se estabelecerem nas manchas. Dado que o *pool* florístico regional contem espécies com sementes grandes e tolerantes ao sombreamento, o tamanho médio das sementes em *c*, *s*(*c*), dependerá diretamente dos atributos de *d*. Se os dispersores que compõem *d* forem espécies de pequeno tamanho corpóreo, *s*(*c*) será limitado por este atributo de *d*, modificando o padrão esperado de colonização de manchas por novas espécies (Fig. 1b). Portanto, não apenas as características do habitat relacionadas ao estabelecimento das plantas deverão ser consideradas no modelo de nucleação florestal, mas também a atratividade do mesmo em relação a diferentes grupos de dispersores.

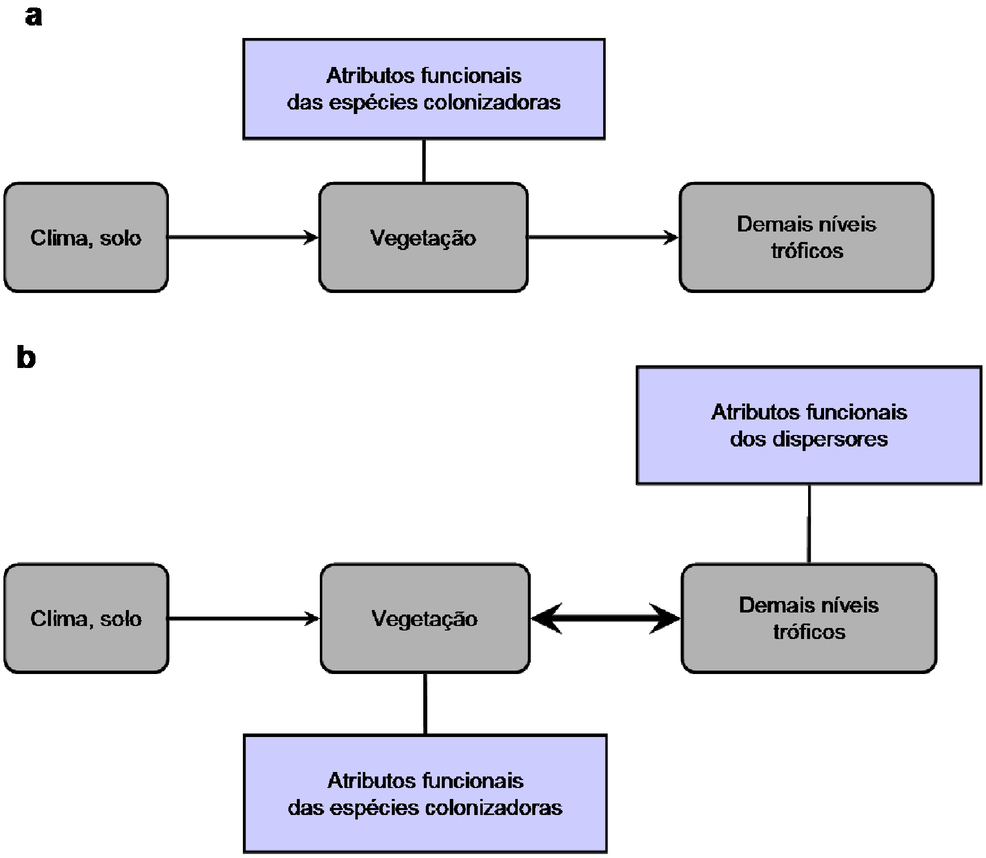

Fig. 1. *Modelos de dinâmica de nucleação de manchas de floresta com* Araucaria *nos campos do Planalto Sul-brasileiro. a) Modelo original de Klein (1960). b) Modelo ampliado.*

Nota final sobre a conservação do mosaico campo-floresta com *Araucaria*

Os resultados obtidos neste estudo ressaltam a importância fundamental da dispersão de frutos e sementes por vertebrados na estrutura e dinâmica de nucleação das manchas de floresta com *Araucaria* em áreas campestres naturais, desde o estabelecimento inicial das espécies sob a copa de plantas-berçário até a colonização de capões florestais mais desenvolvidos. A conservação do ecossistema formado pelos campos do Planalto e pela floresta com *Araucaria* não pode ser assegurada apenas pela manutenção estática de ambientes campestres ou florestais. A dinâmica entre estes dois ambientes associados representa a sua maior riqueza e somente poderá ser devidamente conservada se algum esforço for empreendido, no sentido de garantir a manutenção de populações viáveis das espécies animais presentes no mosaico vegetacional. Em áreas as atividades humanas, como a caça predatória, a criação extensiva de gado bovino, a queimada simultânea sobre extensas áreas de campo, ou mesmo a substituição do campo nativo por monoculturas de lavouras e espécies arbóreas exóticas, inviabilizam a ocorrência de uma parte considerável da fauna nativa ainda restam muitos capões florestais aparentemente bem preservados. Na realidade, são ambientes deteriorados, vazios, onde não se observa quase nenhuma renovação na vegetação madura. São formações vegetais visualmente saudáveis, mas ecologicamente estéreis.

Referências

Clements, F.E. 1928. *Plant Succession and Indicators – A Definitive Edition of Plant Succession and Plant Indicators*. The H.W. Wilson Company, Nova Iorque, EUA.

Daubenmire, R. 1968. *Plant Communities – A Textbook of Plant Synecology*. Harper & Row, Nova Iorque, EUA.

Gleason, H.A. 1939. The individualistic concept of the plant association. *Am. Mid. Nat.* 21: 92-110.

Glenn-Lewin, D.C. & van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. In: *Plant Succession – Theory and Prediction* (Eds. D.C. Glenn-Lewin, R.K. Peet e T.T. Veblen). p. 11-59. Chapman & Hall, Londres, Reino Unido.

Klein, R.M. 1960. O aspeto dinâmico do pinheiro brasileiro. *Sellowia* 12: 17-51.

Silva, J.M.C. & Tabarelli, M. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404: 72-74.

Tansley, A.G. 1949. *Introduction to Plant Ecology – A Guide for Beginners in the Study of Plant Communities*. George Allen & Unwin Ltd. Londres, Reino Unido.