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PULSOS DE INUNDAÇÃO, PADRÕES DE DIVERSIDADE E DISTRIBUIÇÃO DE ESPÉCIES ARBÓREAS EM UMA FLORESTA RIBEIRINHA NO SUL DO BRASIL

JEAN CARLOS BUDKE

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

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"...já me disseram que se acabam as invernadas. Que retalhadas marcam o fim desta existência. Mas trago a essência e a constância de um olho d'água e a alma penduada com sementes de querência..."

Sergio Carvalho Pereira

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Sumário

Resumo

Formações ribeirinhas são áreas de transição entre os sistemas terrestre e aquático, caracterizadas por elevada heterogeneidade ambiental e por um amplo espectro de elementos biológicos e valores socioeconômicos. Contrário às grandes bacias hidrográficas, onde geralmente os pulsos de inundação são sazonais, os rios de pequeno porte apresentam regimes de inundação freqüentemente imprevisíveis, onde os gradientes de perturbação podem ser expressos pela razão direta entre intensidade, duração e freqüência. Considerando a distribuição de grupos ecológicos ao longo de um gradiente de inundação e as relações entre distúrbio e variáveis ambientais, o presente trabalho teve como objetivo avaliar os padrões de riqueza e diversidade de espécies arbóreas em um rio com regime de inundações não-previsível. O estudo foi realizado próximo à foz do rio Botucaraí (30º 01'S e 52º 47'W), em quatro parcelas de 1 ha, situadas em diferentes cotas de elevação. Cada parcela foi dividida em 10 transecções contíguas de 10 × 100 m, paralelas à margem do rio, sendo cada transecção posteriormente subdividida em unidades amostrais de 10 × 10 m. Em cada parcela, todos os indivíduos arbóreos vivos com perímetro à altura do peito (pbh) $\geq$ 15 cm foram amostrados. Coletas superficiais de solo (0 – 20 cm de profundidade) foram realizadas, bem como um detalhamento topográfico das parcelas. A freqüência de distúrbio em cada unidade amostral foi definida a partir da interpolação de cota topográfica de cada unidade amostral com os pulsos de inundação para o período de 1981–2004. Técnicas multivariadas de ordenação e classificação foram aplicadas, a fim de explorar as relações entre distribuição de espécies arbóreas, grupos ecológicos de regeneração, estratificação e dispersão com as variáveis ambientais. Uma modelagem por equações estruturadas definiu um modelo significativo entre freqüência de distúrbio, biomassa e variáveis ambientais sobre a variação na riqueza de espécies. Foram amostrados 5.779 indivíduos arbóreos de 37 famílias botânicas. A interação entre distúrbio e biomassa revelou um pico de riqueza de espécies com o aumento da biomassa e a diminuição da freqüência de distúrbios. O modelo estrutural final explicou 79% da variação na riqueza de espécies e 67% na variação sobre biomassa. A análise dos grupos ecológicos revelou menor estratificação vertical em direção às áreas mais inundáveis. Estas áreas também apresentaram maior proporção de indivíduos de espécies pioneiras e dispersão autocórica. Variações florísticas ao longo do gradiente sugerem que a seleção de habitat influencia os padrões de distribuição das espécies, favorecendo histórias de vida com características generalistas, em decorrência de um regime de inundações não-previsível.

Palavras-chave: Biomassa, distúrbio, fisionomia florestal, grupos ecológicos, modelagem por equações estruturais, regime de inundações, Rio Botucaraí, riqueza e diversidade de espécies.

Abstract

Riverine systems are transitional areas between land and aquatic ecosystems that present high environmental heterogeneity and including a wide array of socio-economic and biological values. In large hydrographic basins, flood pulses are seasonal and currently predicted which differ substantially from small rivers, where flood pulses are unpredictable and should be referred as a direct interaction of intensity, duration and frequency. By analyzing the distribution of ecological groups across a flood gradient and the relationships among disturbance and environmental variables, the present work addressed to analyze tree species richness and diversity in a small river with unpredictable flood regime. The survey was conducted in the lower sector of rio Botucaraí (30º 01'S e 52º 47'W) where we installed four 1 ha plots across different topographical sites. Each plot comprised ten contiguous 10 × 100 m transects, parallels to the river margin and then, each transect was subdivided in 10 × 10 m sampling units. In each plot we sampled all individual living trees having at least 15 cm of perimeter at the breast height (pbh). We collected samples of the topsoil (0–20 cm depth) and we carried out a detailed topographic survey of each plot. We interpolated the topographical position of each sampling unit and inundation records from 1981–2004 to obtain a disturbance frequency to each position. We applied multivariate ordination and grouping techniques to seek for relationships among environmental variables, tree species distribution and ecological groups of regeneration, stratification and dispersal. A structural equation modelling improved a significant model among flood frequency, biomass and environmental variables over species richness. Field inventory yielded a total of 5,779 trees belonging to 96 species and 36 families. The interaction between disturbance and biomass revealed a species richness peak with higher biomass and lower disturbance frequency. The final structural model explained 79% of variance in species richness and 67% of variance in biomass. The ecological groups' analyses revealed lower vertical stratification toward frequently inundated areas. Moreover, these sites presented higher proportion of pioneer and autochorous trees. Floristic changes across the gradient suggest that habitat selection influences species distribution patterns, by selecting generalized live history traits due to the unpredictable flooding regime.

Key words: Biomass, disturbance, Botucaraí river, ecological groups, flood regime, forest physiognomy, species richness and diversity, structural equation modelling.

Organização Geral

Esta tese está organizada em capítulos, os quais constituem artigos independentes, que foram ou serão submetidos à publicação em revistas de circulação internacional. Uma introdução geral e conclusão compõem um todo coerente onde são apresentados os objetivos, o delineamento amostral e as conclusões gerais do trabalho.

O capítulo I descreve o componente arbóreo e as relações com variáveis ambientais em uma área sujeita a inundações freqüentes (área I), onde pequenas oscilações topográficas geram um mosaico vegetacional característico principalmente pela presença de espécies pioneiras.

O capítulo II analisa as relações entre estrutura do componente arbóreo, grupos ecológicos e variáveis ambientais em uma área com freqüência de inundações menor que a anterior. São realizadas comparações entre estas duas áreas quanto aos padrões de riqueza e diversidade e a interferência dos pulsos de inundação.

O capítulo III compara riqueza, diversidade e grupos ecológicos em uma área sujeita a inundações esporádicas (área III) e discute estes parâmetros com relação à seleção ambiental imposta pelas inundações nas áreas mais rebaixadas.

O capítulo IV avalia a estruturação de um gradiente topográfico em relação à freqüência de distúrbios e as conseqüências sobre os padrões de textura e propriedades físico-químicas do solo. Um modelo hipotético relacionando freqüência de distúrbio, produtividade (biomassa), variáveis ambientais e riqueza de espécies arbóreas, foi avaliado, através de modelagem por equações estruturadas.

Introdução

In summo monte Botucurahy

Friedrich Sellow

Formações ribeirinhas são áreas transicionais entre os sistemas terrestre e aquático, arranjadas em redes através da paisagem, incluindo um amplo espectro de elementos biológicos e valores socioeconômicos. Caracterizando-se como sistemas próximos de um equilíbrio dinâmico e promotores de elevada heterogeneidade ambiental, as comunidades biológicas das zonas ripárias freqüentemente estão entre as mais produtivas e diversas do globo (Nilsson & Svedmark 2002).

A América do Sul destaca-se pelo grande volume de águas superficiais, incluindo algumas das maiores bacias hidrográficas do planeta em termos de descarga média anual (Neiff *et al*. 1994). Configuradas como extensas planícies de inundação, entremeadas pela Cordilheira dos Andes e pelos maciços cristalinos da Guiana e Brasileiro, a grande maioria das bacias hidrográficas da América do Sul apresenta pouca concavidade e com isso, baixa vetorialidade (típicos dos rios de montanhas) possibilitando a evolução de diferentes sistemas hídricos, incluindo grandes terraços fluviais, deltas, canais anastomosados e sistemas meândricos (Bigarella *et al*. 2003).

Nestas redes, moldadas em última instância pelos processos hidrogeomorfológicos, a biota distribui-se de acordo com as suas peculiaridades, adquiridas ao longo do processo de seleção natural e refletindo as flutuações climáticas ocorridas ao longo do tempo. A vegetação ribeirinha expressa esta evolução em diferentes níveis, seja na escala de indivíduo, refletida pelas adaptações que possam ocorrer em função da tolerância ou não aos níveis de alagamento; seja em nível comunitário, onde os mosaicos vegetacionais expressam a razão direta entre freqüência e intensidade dos distúrbios.

Mereles (2004) ao descrever os tipos vegetacionais ao longo das áreas úmidas do rio Paraguai (Paraguai), divide-os de acordo com os ambientes predominantes: aquático e palustre-terrícola. Segundo a autora, o porte da vegetação está condicionado à topografia de cada setor: áreas mas rebaixadas e portanto, com a lâmina da água mais próxima da superfície (quando não são áreas completamente submersas) apresentam formas biológicas onde predominam macrófitas aquáticas e *pastizales*[1] (gramíneas e ciperáceas) até aqueles setores onde as inundações possuem uma freqüência sazonal e de menor amplitude, onde predominam formações arbóreas ou arbustivas - *los bosques, matorrales y sabanas* (Mereles 2004). Da mesma forma, as áreas úmidas situadas no setor final do rio Paraná, Argentina (Kandus *et al*. 2002, Kandus & Adamoli 1993) apresentam diferenciações geomorfológicas e hidrológicas, refletindo desde a presença de florestas, nas áreas mais bem drenadas até áreas de *praderas de herbáceas* e *pajonales*, nas áreas mais alagáveis e em alguns casos, em decorrência do fogo.

De maneira geral, os exemplos acima refletem o tempo de permanência que a água permanece sobre o solo, variando de poucos dias até mais de seis meses (Mereles *et al*. 2005). No Brasil, os exemplos clássicos de grandes áreas inundáveis remetem para as *várzeas* da bacia Amazônica e a planície aluvial do Pantanal, apresentando ritmos sazonais (regulares) de alagamento, com períodos alternados de cheia e seca. Por outro lado, existem áreas ribeirinhas com influência fluvial permanente, ou seja, áreas com o solo permanentemente encharcado, não se constituindo eventos de inundação, como o caso das florestas *de brejo, paludosas*, *caixetais* e *igapós*. Rodrigues (2000) propôs uma base nomenclatural com termos e níveis hierárquicos, a fim de classificar as diferentes formações ribeirinhas, relacionando-as basicamente à formação fitogeográfica (base geográfica) e ao regime hidrológico da área (base ecológica). Além desta tentativa, a qual discute algumas denominações existentes nos sistemas de classificação, Ribeiro & Walter (1998, 2001) tratam da classificação das florestas ribeirinhas existentes na região central do Brasil.

À parte das grandes planícies de inundação, uma porção considerável da rede fluvial que alimenta estas grandes massas de água encontra-se em áreas mais elevadas, onde a dissecação do terreno é mais pronunciada e com isso, as áreas inundáveis são progressivamente menores. Muitos rios de grande ordem (porte) no Brasil encontram-se em tal situação geomorfológica, estando encaixados em vales profundos e desta forma, com planícies de inundação muito estreitas, quando presentes.

Pulsos de inundação e evolução de histórias de vida

Do ponto de vista hidrológico, os rios são sistemas abertos, com um fluxo contínuo de elementos dirigindo-se das nascentes para a foz. A água, através do escoamento superficial

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[1]

advindo das chuvas ou pelos lençóis subterrâneos, combina-se para formar canais de pequena ordem, os quais derivam após confluência, gerando canais sucessivamente maiores. A delimitação deste sistema é auxiliada pelas características geomorfológicas da paisagem, onde cada unidade fluvial (bacia hidrográfica) define-se pela direção do fluxo de elementos, como água, sedimentos e seres vivos.

Os rios, como sistemas abertos, possuem fluxos longitudinais, verticais e laterais, os quais abrangem zonas de captação de materiais, áreas de transformação-passagem e, por fim, zonas de estocagem. Os setores iniciais ou de cabeceiras (Fig. 1), também conhecidos por setores erosivos (montante) constituem-se nas principais áreas de produção ou de entrada de materiais (seres vivos, sedimentos) no sistema (Petts 1994). Estas áreas possuem um formato estreito, onde são freqüentes as cachoeiras e corredeiras, não permitindo grandes trocas entre o sistema terrestre e aquático, exceto em eventos de chuvas torrenciais. Por outro lado, o setor de deposição constitui-se em largas planícies de inundação que geralmente correspondem ao baixo curso (jusante) ou porção final da bacia. Nestas áreas, a pequena declividade e o movimento mais lento das massas de água forçam os canais a formarem meandros, gerando depósitos de sedimentos, lagoas internas e leitos abandonados (Ab’Saber 2000, Ward *et al*. 2002). Entre estas duas extremidades, está o setor de transferência ou de transição (Fig. 1), onde se espera encontrar elevada diversidade biológica, devida principalmente à grande heterogeneidade ambiental (Dunn *et al*. 2006). Sem dúvida, o fluxo de informações biológicas e sedimentos dentro dos rios e planícies de inundação está sujeito a uma série de fatores modeladores, onde os eventos de inundação caracterizam-se como a principal força no sistema.

A conectividade existente entre atributos hidrogeomorfológicos faz com que cada bacia possua um regime hidrológico próprio, o qual pode ser expresso pelos níveis/vazões ao longo do ano hidrológico. As inundações, como manifestações claras dos pulsos existentes, são responsáveis pela permanência, produtividade e interações da grande biota verificada nestas áreas (Schwarzbold 2000). Com o desenvolvimento de concepções abrangentes sobre o funcionamento dos rios, que incluíram a dinâmica espacial (“Conceito de Rio Contínuo” - Vannote *et al*. 1981); a dinâmica temporal (“Conceito de Pulso de Inundação” - Junk *et al*. 1989) e o estudo das interações em escalas múltiplas (Poole 2002), os ecólogos de rios combinaram o estudo destes sistemas através da Ecologia da Paisagem, aplicada de forma a operacionalizar os diferentes elementos combinados nesta metaestrutura.

matéria, energia) para o rio

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matéria, energia) para o rio

Figura 1. Entrada de informações no sistema (diagramas laterais) e principais setores de uma bacia hidrográfica, a) setor inicial ou erosivo; b) setor intermediário ou de transição; c) setor deposicional (modificado de Tabacchi *et al*. 1998).

Um grande problema encontrado nos rios e áreas úmidas com movimento horizontal da água é que as trocas de materiais não ocorrem na forma de ciclos (por exemplo, os "ciclos biogeoquímicos" não são ciclos) mas sim na forma de pulsos, com fases de inundação e seca (Neiff 1997). Desta forma, os processos ecológicos fluviais possuem uma variabilidade sujeita às diferenças encontradas entre a *potamofase* (coluna da água acima dos valores da ordenada), onde ocorrem fluxos horizontais de sedimentos, detritos e organismos vivos do leito do rio em direção às laterais (planície de inundação, quando houver) e a *limnofase* ou fase de escoamento, onde as informações são transportadas em direção ao leito principal (Neiff 1997).

Este padrão de variabilidade, determinado por fases distintas gera o regime de pulsos de um rio. Os pulsos de inundações podem ocorrer com amplitude desde a imprevisibilidade à previsibilidade e de curta à longa duração (Schwarzbold 2000). Em grandes bacias hidrográficas, as flutuações dependem sensivelmente dos eventos na parte superior da bacia, geralmente a longas distâncias. Na América do Sul, os rios da bacia Amazônica, do complexo do Pantanal e da bacia do Paraná refletem estas características, havendo duas fases regulares (sazonais) durante o ano hidrológico, uma aquática e outra terrestre. No rio Amazonas, o período de inundação pode ser superior a 210 dias por ano (Parolin *et al*. 2004). Por outro lado, rios de pequeno porte (baixa ordem) possuem regime de inundação definido especialmente pelas chuvas que ocorrem à montante e de influência local, como chuvas torrenciais. Estes eventos podem gerar episódios de inundação breves ou longos, de acordo com a região de ocorrência e a capacidade de drenagem da bacia, entretanto, são quase sempre imprevisíveis.

Ao longo de um gradiente de distúrbio, os organismos vivos apresentam padrões de distribuição conferidos a partir de diferentes atributos próprios (história de vida, comportamento reprodutivo e morfologia, por exemplo) somados aos componentes estocásticos do sistema, os quais tornam aptos à presença (e a forma de distribuição) ou ausência de uma espécie em determinada área (Lytle & Poff 2004). Estas características fazem com que as espécies estejam relacionadas à potamofase, limnofase, ou, à capacidade de se distribuir em uma ampla gama de condições do regime pulsátil (Neiff 1997), sendo que diferentes características de uma fase podem ser mais ou menos importantes a uma espécie. Neste sentido, um organismo pode ser mais tolerante a duração de uma inundação e menos tolerante à magnitude do evento.

De acordo com este princípio, Neiff (1990) propôs a função *f* FITRAS, que reúne os principais atributos de um pulso: freqüência, intensidade, tensão, regularidade, amplitude e estacionalidade, os quais se inter-relacionam e estarão interferindo nos padrões de distribuição dos organismos. A função *f* FITRAS possui atributos temporais (freqüência, recorrência e estacionalidade) que estão relacionados ao comportamento histórico dos atributos espaciais (amplitude, intensidade e tensão), que definem os efeitos do pulso sobre a área inundada (Neiff 1990).

Áreas com inundações sazonais, como verificado na bacia Amazônica, Orinoco e complexo do pantanal (entre outras) caracterizam-se especialmente pela nitidez verificada entre a ocorrência das fases de pulso (previsibilidade), comferindo elevada recorrência e estacionalidade a estas áreas. Em decorrência, muitas espécies apresentam sincronismos com a época de cheia ou de seca, que incluem a época de reprodução ou produção de biomassa, oriundas a partir da seleção exercida sobre a história de vida destes organismos (Lytle & Poff 2004). Exemplo clássico são os eventos fenológicos de diversas espécies de várzeas da Amazônia, as quais apresentam novas folhas ao final do período de cheia e com pico durante a limnofase; por outro lado, o florescimento de muitas espécies ocorre no começo da época das cheias, e a produção de frutos pouco tempo depois, sendo os propágulos dispersados pela água e pela fauna aquática (Parolin *et al*. 2002, Parolin *et al*. 2004). No alto rio Paraná, onde a sazonalidade é menor do que no exemplo acima (os picos de inundação variam de outubro a janeiro e estendem-se de março a abril do ano subseqüente) verifica-se que diversas espécies de peixes possuem um sincronismo reprodutivo associado à temperatura e duração do dia (Vazzoler *et al*. 1997). Muitas destas espécies são migratórias e têm o início da fase de cheia como um sincronizador para a desova, quando as condições de alimentação são excepcionais (Benedito-Cecílio & Agostinho 2000).

Nem todos os regimes de inundação favorecem a evolução de características particulares que facilitem a sobrevivência a inundações ou secas (Lytle 2001). Segundo a teoria de histórias de vida, a magnitude, freqüência e previsibilidade dos distúrbios afetam a forma como as populações se adaptam ou são eliminadas por estes eventos. Quando os eventos são freqüentes, de grande magnitude e previsíveis, a seleção favorece histórias de vida que são sincronizadas a evitarem ou explorarem estes eventos extremos (a chamada zona evolucionária) (Junk *et al*. 1989, Walker *et al*. 1995). Por outro lado, eventos de distúrbio que são de grande magnitude e freqüentes, porém de baixa previsibilidade geram alta mortalidade sobre as populações (zona ecológica) (Litle & Poff 2004). Porém, ambos os regimes terão influência sobre as populações de acordo com o tempo de vida de cada uma das espécies.

Riqueza, diversidade e gradientes ambientais

Diversas hipóteses têm sido formuladas para explicar os padrões de diversidade de plantas em escala local, sendo que em muitas delas, o papel de distúrbios naturais e estresses abióticos tem sido enfatizados (Pausas & Austin 2001). Certamente, a existência de pulsos de inundação promove alterações locais que variam no espaço e no tempo, gerando gradientes de perturbação que podem ser expressos pela razão direta entre intensidade, duração e freqüência.

Grace (1999) realizou uma revisão sobre as teorias relacionadas aos gradientes de produtividade, distúrbio e número de espécies em comunidades de plantas herbáceas e verificou a complexidade da literatura sobre o assunto, onde mais de 100 teorias já foram apresentadas, descrevendo sobre a diversidade de espécies em escala local. Em áreas com baixa disponibilidade de recursos ou elevado estresse e distúrbio, a diversidade e produtividade são geralmente baixas, pois, somente poucas espécies conseguem se manter nestas condições. Com o aumento na oferta de recursos ou decréscimo no estresse ou distúrbio, diversidade e produtividade tendem a aumentar até um certo grau, a partir do qual, apenas poucas espécies, altamente competidoras, tornam-se dominantes e suprimem as outras (Tilman 1982).

Os modelos baseados em hipóteses univariadas (riqueza de espécies como função unimodal de produtividade ou distúrbio) tiveram algum sucesso em explicar os padrões de diversidade, particularmente em estudos onde as unidades amostrais variavam num único fator explicativo (Cardinale *et al*. 2006). Entretanto, trabalhos recentes têm reconhecido que modelos baseados em um único fator causal são freqüentemente inadequados em explicar os padrões de diversidade em escala local (Molino & Sabatier 2001).

Um dos primeiros modelos propondo que a diversidade era resultado do equilíbrio dinâmico entre as taxas de produção de biomassa (exclusão competitiva) e regimes de distúrbio (diminuição da competição entre espécies) foi desenvolvido por Huston (1979). Após uma série de estudos sobre tais parâmetros (Huston 1979, 1994, Pollock *et al*. 1998), Kondoh (2001) aprimorou este modelo, atribuindo o caráter unimodal às relações entre riqueza de espécies e distúrbio-produtividade, mas, o nível de um fator que maximiza a riqueza de espécies dependia do nível do segundo fator, numa interação que gerava padrões não reconhecidos pelos modelos univariados (Cardinale *et al*. 2006). De acordo com Cardinale *et al*. (2006) uma vantagem deste modelo é que a coexistência de espécies possui mecanismos plausíveis, necessitando de distúrbios para criar novas oportunidades de nicho no espaço e no tempo. Assim, novas oportunidades podem resultar quando distúrbios pontuais fazem com que as populações expressem de forma diferenciada seus padrões de história de vida, como a habilidade em competir por recursos limitantes ou colonizar novos espaços. Segundo estes autores, a expressão das histórias de vida é também uma função da produtividade, a qual influencia a taxa de acumulação de biomassa em áreas abertas, dispersão de propágulos através de mosaicos e, finalmente, a velocidade de reposição entre competidores. Como resultado, distúrbio e produtividade juntos determinam uma variedade de histórias de vida que podem ser expressas num sistema.

Adaptações das plantas à inundação

Os eventos de inundação geram diferentes impactos sobre as populações de plantas distribuídas em zonas ribeirinhas, incluindo mudanças morfológicas, anatômicas e fisiológicas (Koslowski 2002). Além disto, o alagamento influencia profundamente as características do solo, diminuindo as trocas gasosas entre solo e ar e conseqüentemente, interferindo em processos no desenvolvimento vegetal. O acúmulo de gases (N_2, CO_2 e H_2), produção de hidrocarbonetos, compostos fenólicos, álcoois e ácidos graxos voláteis devido à anaerobiose; aumento de pH em solos ácidos e sua redução nos alcalinos e diminuição significativa do potencial redox, são algumas dessas conseqüências (Koslowski 2002, Medri *et al*. 2002). A variação na freqüência e intensidade no processo de alagamento irá determinar características abióticas particulares, tanto em nível edáfico quanto micro- climático, interferindo nos processos biológicos como decomposição e estabelecimento de indivíduos (Lobo & Joly 2000).

As respostas das plantas ao alagamento são muito variadas e dependem do estádio de desenvolvimento do indivíduo. Mudanças morfológicas e anatômicas incluem a hipertrofia de lenticelas, formação de raízes adventícias, hipertrofia da base dos caules, redução do crescimento e do desenvolvimento das plantas, senescência, abscisão e epinastia foliar (Medri *et al*. 2002). Por outro lado, as mudanças ecofisiológicas incluem alterações nas rotas metabólicas na produção de energia e mecanismos de difusão de O_2 para a rizosfera (Lobo & Joly 2000). Entretanto, de acordo com estes autores, o estudo isolado de respostas metabólicas e morfo-anatômicas à saturação hídrica do solo não permitem a classificação das espécies em tolerantes ou intolerantes ao alagamento, pois, a indução ao desenvolvimento destas modificações pode ser uma mera resposta a alterações significativas dos processos de síntese e/ou translocação de hormônios como auxina e etileno, sem proporcionarem um aumento na difusão de O_2 para o sistema radicular, ou seja, não possuiriam valor adaptativo. Ferreira & Ribeiro (2001) revisaram uma série de trabalhos sobre mecanismos de tolerância das plantas à inundação, bem como Lobo & Joly (2000) e Medri *et al*. (2002), havendo o consenso de que duas principais estratégias ocorrem em condições hipóxicas: aumento de disponibilidade de O_2 através da difusão do oxigênio da parte aérea para o sistema radicial e; redução ou alteração das taxas metabólicas para evitar o acúmulo e/ou a síntese de compostos tóxicos.

Vazão ambiental e funcionamento ecológico dos rios

O ambiente ribeirinho freqüentemente se reflete em mosaicos vegetacionais devido à grande heterogeneidade encontrada nestas áreas. As características hidrogeomorfológicas, atuando como modeladores constantes da paisagem, geram padrões complexos de interações entre os organismos. Os padrões emergentes resultantes de toda esta dinâmica freqüentemente escapam aos instrumentos de mensuração do pesquisador, pela falta de uma análise integrada de seus processos constituintes. Rodrigues & Shepherd (2000) apontaram os principais elementos que condicionam a estruturação de florestas ribeirinhas, ressaltando a importância dos modelos integrados de estudo para a adequação de propostas de conservação, manejo e recuperação destas áreas.

Naiman & Décamps (1997) definem as áreas ribeirinhas como sistemas de transição entre os ambientes terrestre e aquático, onde diferentes situações podem conter características particulares, sejam estruturais ou dos grupos constituintes. Por outro lado, em se tratando de grandes planícies de inundação, Neiff (1997) e Neiff *et al*. (1994) sustentam que estas áreas funcionalmente não se comportam como áreas transicionais, reconhecendo uma identidade própria a estes ambientes. Estas duas definições, concebidas em dois ambientes diferenciados, claramente refletem a dificuldade de interpretação sobre os aspectos funcionais dos sistemas ribeirinhos. Desde as nascentes e riachos de áreas montanhosas até grandes áreas úmidas, característica importante das porções finais de uma rede fluvial, existe um *continuum* de variações que dificulta a definição precisa de onde começa e onde acaba cada situação.

A vazão ecológica ou vazão de proteção ambiental define-se pela vazão hídrica necessária para que sejam preservados os processos geradores de pulsos hidrológicos e movimentação de informações ao longo da bacia hidrográfica, permitindo a manutenção das populações biológicas e o funcionamento do ecossistema ribeirinho (Cruz 2005). Sendo um dos elementos legais da legislação brasileira para a integridade destas formações, necessita de uma abordagem integrada para uma coerente tomada de decisões sobre a outorga da água e as conseqüências destas ações sobre a integridade da paisagem ribeirinha.

Objetivo geral e hipótese inicial

Esta tese tem como objetivo geral avaliar os padrões de riqueza e diversidade de espécies arbóreas ao longo de um gradiente de distúrbio ocasionado por variações na freqüência de inundações, considerando a distribuição de grupos ecológicos ao longo do gradiente de inundação e as relações do distúrbio sobre variáveis ambientais, especialmente solo. A hipótese deste estudo é que em florestas ribeirinhas com inundações não-previsíveis, a seleção de hábitat favorece o estabelecimento de espécies generalistas, sendo que a riqueza de espécies tende a aumentar em direção às áreas com menor freqüência de inundações.

Área de estudo e delineamento amostral

Caracterização da paisagem e clima

O rio Botucaraí inicia-se na região do planalto Sul-Brasileiro, com direção norte-sul, juntando-se ao rio Jacuí, na Depressão Central (Fig. 2). A região do estudo insere-se no Domínio Morfoestrutural das bacias e coberturas sedimentares, apresentando baixa declividade e predominando as formas suaves (Justus *et al.* 1986). O clima regional é do tipo Cfa (Fig. 3), segundo a classificação de Köppen, ou seja, subtropical úmido, sem período seco, com a temperatura média anual de 19,2ºC, sendo a média do mês mais quente superior a 24ºC e a média do mês mais frio em torno de 13ºC, com precipitação de 1.594 mm.ano^{-1} (IPAGRO 1992). A vegetação predominante na região é a Floresta Estacional (Lindenmaier & Budke 2006).

O alagamento, ocorrente na região devido a chuvas torrenciais, interfere principalmente nos rios de pequeno porte (baixa vasão), como o rio Botucaraí, pela pequena capacidade de escoar o excedente hídrico, ou então, nas proximidades da foz, pelo represamento junto a um rio de maior porte (Aveline 1944). Segundo Schreiner (2003), a bacia do rio Botucaraí apresenta um coeficiente de compacidade e fator de forma que indicam a propensão da bacia em sofrer alagamentos, bem como a presença de caixa de pouca profundidade, a qual leva a um baixo escoamento, os quais intensificam os alagamentos nos trechos que serpenteiam regiões de planície (Fig. 4).

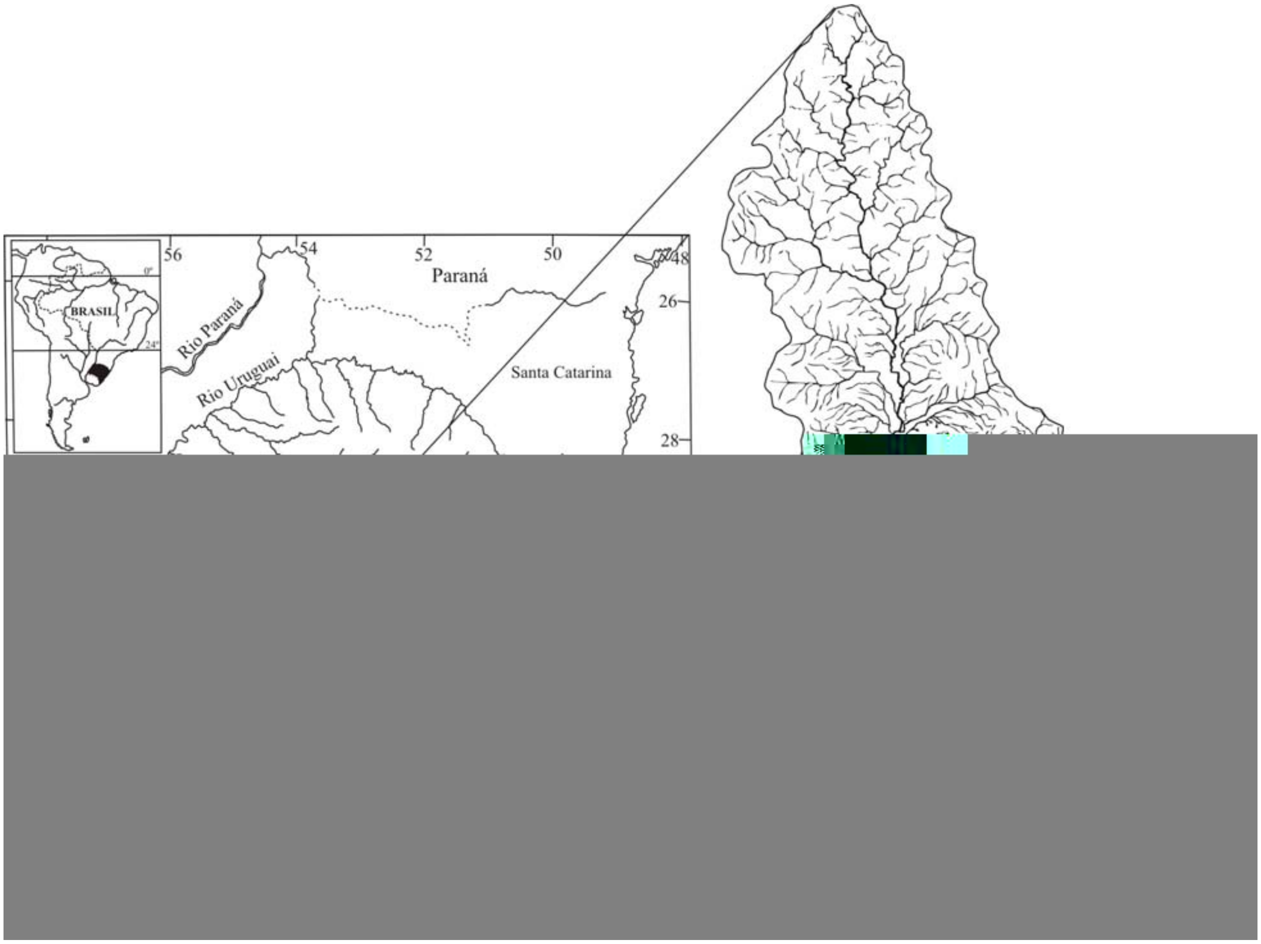

Figura 2. Localização da área de estudo, próximo à foz do rio Botucaraí, sul do Brasil.

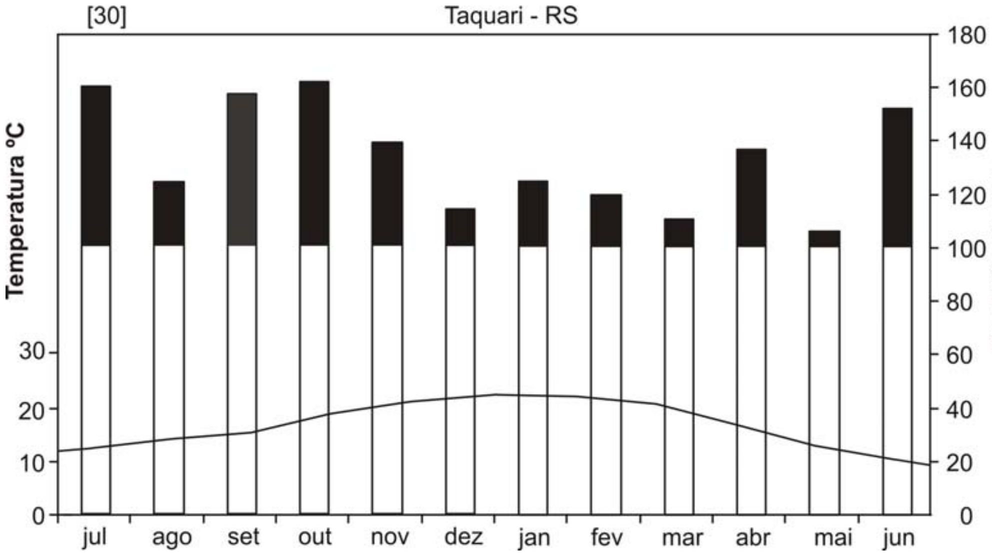

Figura 3. Diagrama climático da região de Taquari, sul do Brasil, entre o período de 1976 a 2005.

Ao longo dos setores médio e final do rio Botucaraí, extensas plantações caracterizam a região, predominando a cultura do arroz. Nestas áreas, o fornecimento de água durante o desenvolvimento da cultura provém do leito principal do rio, ou então, através de barragens de pequeno e médio porte, construídas ao longo das áreas de cultivo (Fig. 5).

Os solos da região variam de acordo com a posição topográfica do terreno. Nas áreas mais elevadas classificam-se como Argissolo vermelho da unidade de mapeamento Rio Pardo (Streck *et al*. 2002), sendo profundos e bem drenados. Próximo à área de estudo IV (mais elevada), ocorrem depósitos de seixos de quartzo, relacionados à dinâmica sedimentar do Rio Jacuí. Dirigindo-se para as áreas mais baixas, predominam os Planossolos hidromórficos (Streck *et al*. 2002), já associados com a dinâmica de inundação dos rios Jacuí e Botucaraí. Nestas áreas, podem ocorrer Neossolos Flúvicos, principalmente nas áreas de contato mais efetivo com as calhas dos rios, onde a dinâmica sedimentar forma camadas estratificadas não relacionadas, onde podem se intercalar sedimentos, serapilheira e outros materiais oriundos da dinâmica hidrosedimentar (Fig. 6, Fig 7).

Procedimento amostral e analítico

Foram escolhidas quatro áreas localizadas em diferentes cotas de elevação em relação ao nível médio do rio Botucaraí. As três primeiras áreas situam-se próximas à margem do rio, entretanto, diferem pela altura média do dique marginal, o que ocasiona variações quanto às inundações que atingem cada área. Uma quarta área foi incluída no estudo e trata-se de um fragmento localizado a cerca de 2.000 m de distância do rio Botucaraí, sendo uma área não sujeita a inundações. Este fragmento foi estudado quanto às características estruturais do componente arbóreo por Lindenmaier & Budke (2006).

Em cada área, foi instalada uma parcela de 1ha (100 × 100), subdividida em unidades amostrais contíguas de 10 × 10 m, a fim de permitir a análise dos dados em diferentes escalas (ver capítulo 4). Em cada parcela, foram amostrados todos os indivíduos vivos de espécies arbóreas com perímetro à altura do peito ≥ 15 cm, sendo mensurado o perímetro de cada indivíduo e estimada a altura por comparação a uma vara com podão de coleta de 5 m. A identificação botânica de cada indivíduo procedeu-se *in loco*, ou em laboratório, através de uso de literatura especializada ou por comparações de amostras coletadas com exsicatas identificadas da coleção do Herbário ICN. Indivíduos que apresentaram material fértil foram coletados, herborizados e incorporados ao acervo do Herbário ICN.

Em cada parcela, realizou-se um levantamento topográfico através de mangueiras de nível (Cardoso & Schiavini 2002). Os pontos de leitura foram demarcados a cada 5 m, nas bordas de cada unidade amostral, gerando uma sobreposição de 400 quadrículas em cada uma das 100 unidades amostrais. A partir das cotas topográficas dos pontos de leitura, que continham as distâncias verticais em relação ao nível do rio, foi calculada a cota média de altura em relação ao nível do rio, obtida a partir da média dos nove pontos de leitura existentes em cada unidade amostral (Oliveira-Filho *et al*. 1994).

A caracterização do hidrograma foi realizada através dos dados diários de leitura efetuados no rio Jacuí (ponto de leitura cerca de 12 km da área de estudo). Para se verificar a correlação entre os hidrogramas do rio Jacuí e Botucaraí, realizaram-se correlações entre estes dados e uma série hidrológica obtida por Schreiner (2003) para o ano hidrológico de 2001-2002, próximo à área de estudo. Após comparação, verificou-se uma correlação significativa (r = 0, 92, $P < 0{,}001$). A série de dados utilizada neste estudo abrange os anos de 1981 a 2004, onde foram quantificados os eventos de inundação e posteriormente, interpolados a cada uma das unidades amostrais.

Foram coletadas amostras compostas de solo, totalizando 15 coletas superficiais (0-20 cm de profundidade) por parcela. O material coletado foi acondicionado em embalagens plásticas e transportados para o Laboratório de Análises do Departamento de Solos, Faculdade de Agronomia – UFRGS, onde foram processados e obtidos variáveis físico-químicas, conforme metodologia de Tedesco *et al*. (1997).

Para cada parcela, estimaram-se os parâmetros fitossociológicos de densidade, freqüência, dominância, bem como o índice de valor de importância (Mueller-Dombois & Ellenberg 1974). A diversidade entre parcelas ou entre grupos de unidades amostrais foi comparada através de índices de diversidade de Shannon e Equabilidade de Pielou (Zar 1996). A riqueza de espéceis foi comparada entre áreas ou grupos de unidades amostrais através de curvas de rarefação (Gotelli & Colwell 2001). De acordo com os objetivos do capítulo, técnicas multivariadas de ordenação e agrupamento e modelagem por equações estruturais foram aplicadas, utilizando os pacotes estatísticos AMOS (Arbuckle & Wothke 1999), CANOCO (ter Braack & Smilauer 1998), Multiv (Pillar 2006) e PC-Ord (McCunne & Mefford 1997).

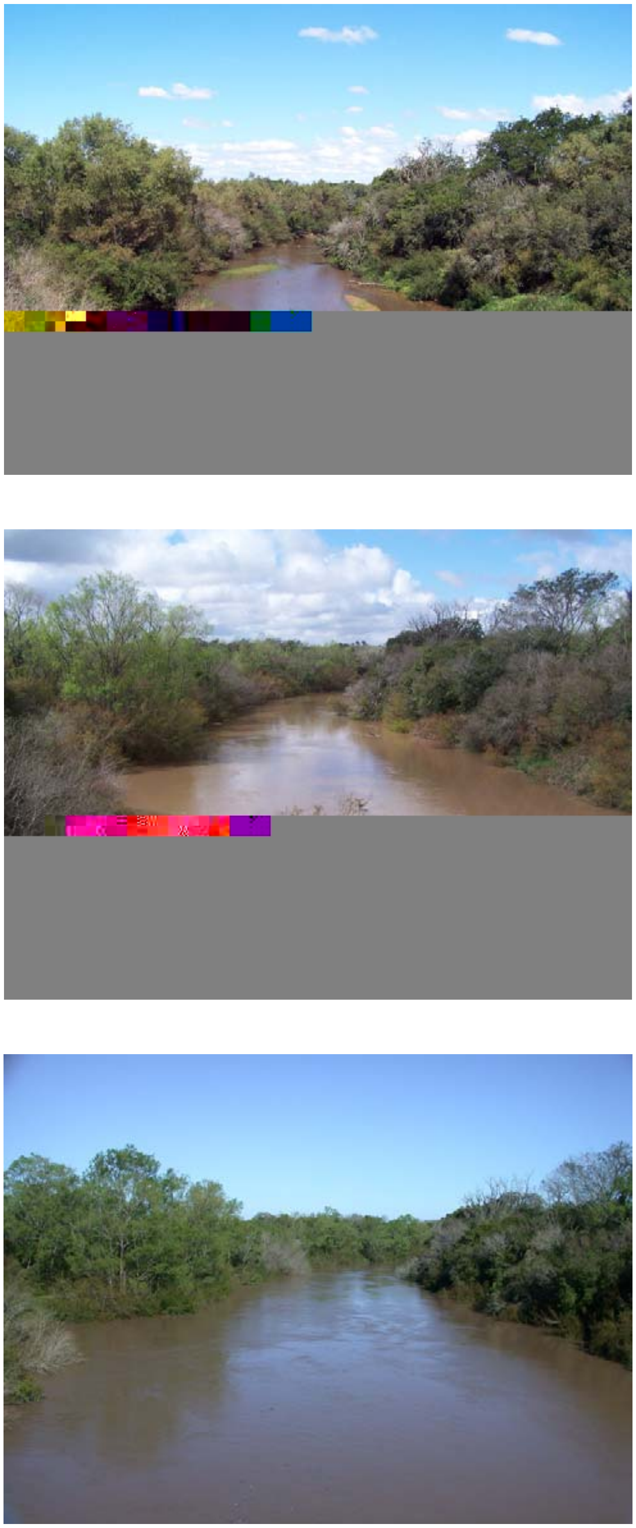

Figura 4. Diferentes fases do regime hidrológico no setor intermediário do rio Botucaraí, sul do Brasil. (Fotos: J.C.Budke & E.L.H.Giehl).

Figura 5. Região do baixo Rio Botucaraí, sul do Brasil. Áreas adjacentes com agricultura intensiva e criação de gado bovino. (Foto: J.C.Budke).

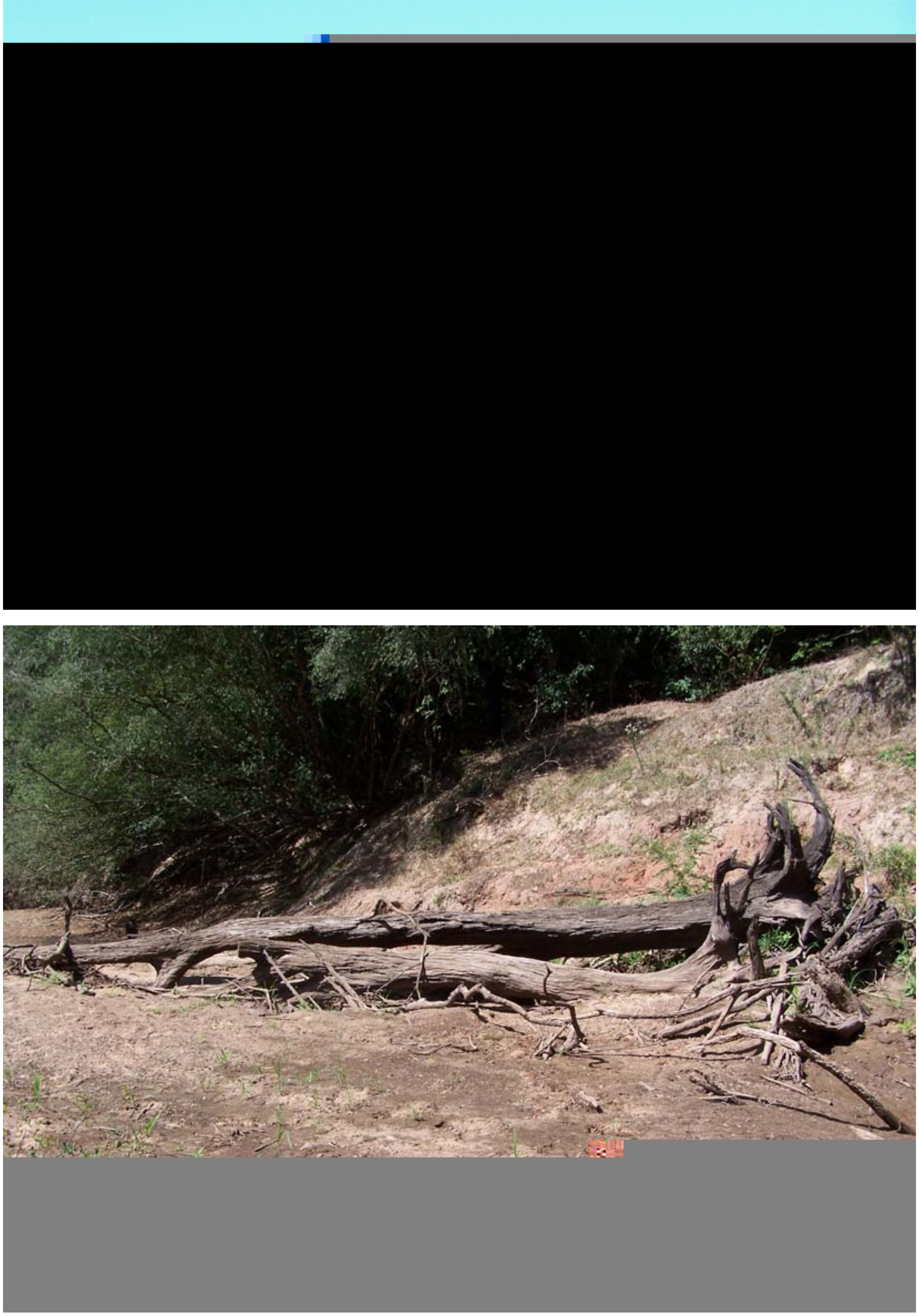

Figura 6. Fragmento florestal (área IV) situado em áreas com atividade orizícola (acima). Área do terceiro levantamento, durante período de seca em 2005 (abaixo), rio Botucaraí, sul do Brasil. (Fotos: J.C.Budke).

Figura 7. Área do terceiro levantamento, durante período de seca em 2005, rio Botucaraí, sul do Brasil (Foto: J.C.Budke).

Capítulo I

Relationships between tree component structure, topography and soils of a riverside forest, Rio Botucaraí, Southern Brazil[2]

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Abstract

The relationships among floristic, structural and physiognomic variables of the tree component, flooding regime variations and soil fertility were investigated in a riparian forest fragment (ca. 43 ha) in the Rio Botucaraí watershed near the confluence with the Rio Jacuí, southern Brazil. All the trees with a dbh ≥ 15 cm were surveyed in 100 contiguous 10 × 10 m plots and soil chemical and textural variables were obtained from the analyses of 15 topsoil samples (0-20 cm depth) collected at different locations. The sample sites encompass all the topographic variation of the area. We used canonical correspondence analysis (CCA) to seek correlations between environmental variables and tree component distribution. The 1,547 surveyed individuals belonged to 30 species and 16 botanical families. The Shannon diversity index (H') and the Pielou equability (J') were 1.995 nats. ind.$^{-1}$ and 0.586, respectively. *Sebastiania commersoniana*, *Casearia sylvestris*, *Eugenia uniflora* and *Eugenia hiemalis* presented the highest importance values. Species' densities chiefly correlated with site elevation, flooding regime and soil chemical fertility. The analyses of ecological categories revealed that most species are heliophylous and typical of early sucessional stages. Richness and diversity ($P < 0.001$) variations from different topographic positions reflect that at the local scale, flooding was a limiting factor for the establishment of certain species suggesting that local processes control species richness and diversity.

Key words: Canonical correspondence analysis, Flooding, Phytogeography, Riverine forest, Vegetation survey.

Introduction

Although riverside environments are protected by legislation in Brazil, riparian forests have been widely clear-cut, due to agricultural land expansion and/or timber and charcoal industries (van den Berg and Oliveira-Filho 1999; Sparovek et al. 2002). Several studies were carried out in the sparse remnants of this unique environment to understand the relationship between plant species distribution and landscape, providing information for sustainable use and conservation (Oliveira-Filho et al. 1994; Metzger et al. 1997; Bianchini et al. 2003; Budke et al. 2004b; Damasceno-Junior et al. 2005). Nevertheless, the effects of flood disturbances on plant community structure remain poorly studied (Ferreira & Stohlgren 1999).

Riparian zones are defined as all the land extending from the floodplain to the adjoining slopes, from stream margins to the drainage basin divides (Tabacchi et al. 1998) and they are characterized by a large spatial heterogeneity that may promote high species richness and diversity (Nilsson & Svedmark 2002). Changes in topographical features, edaphic factors and flood intensity can produce patterns of plant species distribution and affect the structure of riparian plant communities (Oliveira-Filho et al. 1994). This is particularly evident in disturbed areas, where flooding restricts the establishment and growth of several species (Menges and Waller 1983).

Current studies with herbaceous plant communities in wetland zones (Kandus and Adámoli 1993; Kandus and Malvárez 2004) or herbaceous population distribution in riverside forests (Budke et al. 2004a) have proposed that flood level dynamics and the resulting permanence of such waters on topsoil are the principal factors that may be regulating the structure and physiognomy of these sinuses. The same pattern has been described for tree species, where tolerant species would be favored and have increased density or growth rates, while others would just be distributed where flooding is not a limiting factor (Schiavini 1997).

In Amazonian riparian forests, King (2003) recognized that several early successional species depend on the formation of newly cleared or open sites for the establishment and maintenance of the forest landscape. Furthermore, periodically flooded areas were dominated by a few tolerant species, which were rare or absent in well-drained formations. Damasceno-Junior et al. (2005) and Oliveira-Filho et al. (1994) found the same pattern on the floodplains of the Rio Paraguay and Rio Grande, respectively. In contrast, Ferreira and Stholgren (1999) showed that as the scale increased, differences between habitat types weakened in floodplain forests in Central Amazonia. However, the authors agree high species overlap among habitat types suggests many of the species are habitat generalists.

Do changes in both flooding variation and frequency possibly increase mosaician structure in a forest that is set on a terrain with a great surface variation and consequently, sediment deposition? To answer this question, we carried out a survey of topographic, soil and tree species on a riverine forest area of the Rio Botucaraí watershed, in Rio Grande do Sul, southern Brazil. Through these surveys the analysis of the relationships among floristic, structural and physiognomic variables of the tree component, flooding regime variations, soil fertility as well as the comparison of these results with other studies was conducted to enhance the knowledge of riverside environments.

Methods

Study site

The studied forest fragment has an area of ca. 43 ha and is located in the Rio Botucaraí basin, near the confluence of Rio Jacuí (Figure 1); the central coordinates are 30º 01´S and 52º 47´W and mean altitude is 45 m a.s.l. The forest remnant is totally within the municipality of Cachoeira do Sul. The site belongs to the Central Depression physiographic region distributed in the mid sector of the southernmost Brazilian state of Rio Grande do Sul. This region defines the southern limits of the sedimentary, predominantly plain and low altitude terrains of the Paraná Basin (Justus et al. 1986). According to Teixeira et al. (1986), the predominant vegetation is seasonal deciduous forest.

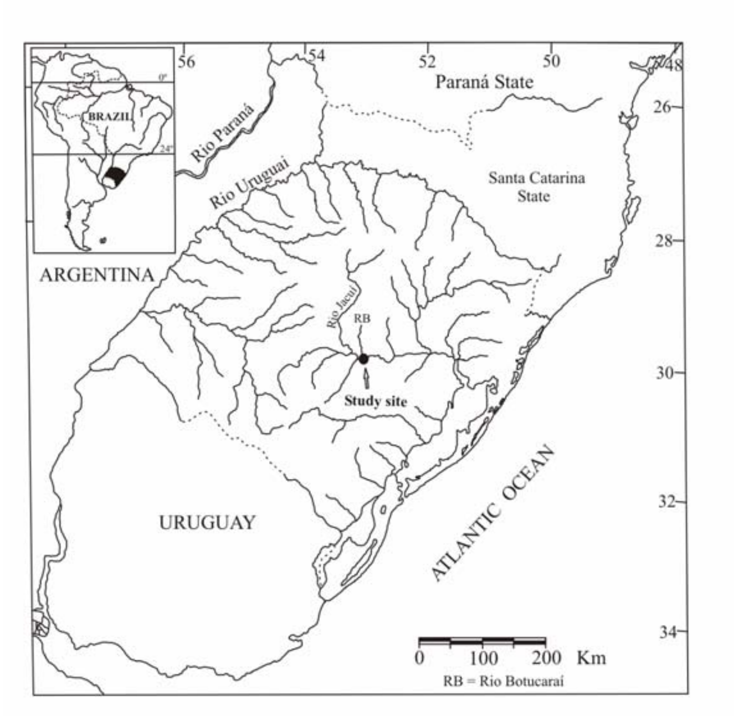

Figure 1. Location of the study site surveyed on the margins of Rio Botucaraí, Cachoeira do Sul, Southern Brazil.

This floodplain environment is also host to large rice-crop farming. Flooding events occur specially in rivers that have smaller channel widths and discharges, such as the Rio Botucaraí, or at streams where the confluence with a stronger adjoining stream flow is blocked by debris and/or sediment buildup, hindering a complete discharge and, thus, promoting lateral extravasations (Aveline 1944; Tabacchi et al. 1998). According to Schreiner (2003), besides being a shallow stream flow, the Rio Botucaraí basin presents a form factor that enhances its flooding tendency.

According to Köppen´s classification, the climate is subtropical humid without a dry season; the mean annual temperature and precipitation are 19.2 ºC and 1,594 mm.year^{-1}, respectively (Moreno 1961). Occasionally, intense rainy periods may produce high river levels that, in turn, promote flooding events. The soils are classified as Hydromorphic Planosols (Streck et al. 2002), that have altering stratified sediment depositional layers according to the terrain.

Vegetation structure

We performed a tree survey in 100 contiguous 10 × 10 m plots that represented the range of both vegetation and topography and subsequently adding the variation of flooding. All individuals with stems, having at least one branch girth of 15 cm or more at breast height (1.3 m above the ground) were measured. Voucher specimens of the different species were collected, prepared and lodged in the Herbarium ICN of the Universidade Federal do Rio Grande do Sul (UFRGS). The species identification was done by consulting the ICN collection, specialized bibliography and specialists. The species were classified into families as recognized by the Angiosperm Phylogeny Group II (APG II 2003).

Topographic survey and soil analysis

Following the protocols in Cardoso and Schiavini (2002), we made detailed topographic surveys of each sample using a 10 m long water-filled leveling hose, 3/8 in., tape measurer, and magnetic needle. The points were obtained every 5 × 5 m, from the center of each plot. This procedure generated a map of vertical contours with 400 subplots. By combining the vertical distances at the river's mean level, we obtained two landform variables for each plot. Variable one was "average elevation" the mean of the vertical levels at nine points in each plot that included the centre, the corners and the middle points. Variable two was "elevation range" which encompassed the differences between the highest and the lowest vertical levels of each plot (Oliveira-Filho et al. 1994).

We obtained soil chemical and textural characteristics from the analyses of 15 superficial topsoil (0-20 cm depth) samples collected at different positions in such way to encompass all topographic variation on the area. Chemical and granulometric analysis of these samples was done at the Faculdade de Agronomia-UFRGS Soil Laboratory. The obtained soil variables were: pH in water suspension, levels of potassium (K

Data analysis

We described the vertical and horizontal distribution of the species using phytosociological parameters (Mueller-Dombois and Ellenberg 1974) for each subgroup. Shannon diversity index (H') and Pielou evenness (J') were used to compare the species diversity of eutrophic and distrophic stands (Zar 1996). The Shannon diversity indexes of the two stands were compared with Hutcheson's t test (Zar 1996). Frequency distributions into classes of diameters and heights were prepared for each stand. In the case of diameter classes, we employed an exponentially increasing range to compensate the normally steep decrease in the density toward larger diameters (Oliveira-Filho et al. 2001). The diameter and height tree frequency distributions were tested for independence with chi-square (χ^2) tests for contingency tables (Zar 1996).

In order to investigate the relationships between species abundances and environmental variables, a canonical correspondence analysis, CCA, was employed (ter Braack 1987), using the software PC-ORD 3.0 (McCune and Mefford 1997). As required by CCA, we set the data into two distinct matrices: the species matrix and the matrix of environment variables. The species matrix contained tree counts per species, per plot. Species with less than ten individuals were deleted, resulting in a 16 species per 100 plots matrix. The abundance values were log-transformed prior to the ordination in order to attenuate effects of the few larger values (ter Braack 1995). The environmental variables matrix included initially all chemical and granulometric figures, the topographic variables (average elevation and elevation range) and an ordinal (ranking) variable, labeled "flooding frequency". We obtained the last variable indirectly from the topographic survey, summarizing flood occurrences and their intensity in each plot. Flooding frequencies embody average elevations, relating to stream flow, the presence of ponds, smaller streams and other features that could intensify flood processes. This variable was set to range from 1 to 4, being: 1 = rare, 2 = sporadic, 3 = occasional and 4 = frequent. All values expressed as a percentage were transformed by the arcsine ($p^{1/2}$) expression. After a preliminary CCA analysis, we eliminated 12 poorly correlated variables or highly redundant ones (indicated by their variance inflation) factors. The six variables remaining in the final CCA were "average elevation", "flooding frequency", pH, potential acidity (Al+H), base saturation (V) and Ca levels. We tested the correlation significance between matrices with Monte Carlo permutation (ter Braack 1987) with 1,000 iterations. To verify the correlations between species and the final six environmental variables, Spearman's rank correlation coefficients were employed (Zar 1996), for species abundance counts and variables values, for each plot.

Ecological classification of the species

We employed an ecological classification of the species to summarize or to search for ecological differences between the two stands. We define three species groups according to the growth conditions for their seedlings (Swaine and Whitmore 1988): (a) pioneer - species with an exclusive heliophylous life cycle, (b) light-demanding climax species and (c) shade-tolerant climax species. Within this arrangement, light-demanding and shade-tolerant species ranged from a continuum of solar radiation, required by the plants for establishment from the juvenile or seed banks (Oliveira-Filho et al. 1994). Additionally, we created a tree-species stratification guild based on the strata commonly reached by the adult individuals: (a) understorey species, (b) canopy species and (c) canopy-emergent species (modified from Swaine and Withmore 1988).

Results

The study site ranged from 45 to 50 m a.s.l. and showed topographic variations that included shallow ponds, flood channels and meanders, all of which enlarged during flood events. Chemical and textural analyses of the soils (Table 1) indicated the presence of one main soil group, Hydromorphic Planosols, with two subgroups according to chemical fertility: distrophic and eutrophic. The distrophic soil subgroup occurred in 39 poorly drained plots with mean texture, elevated clay-levels and lacked a clearly defined horizon with stratified layers of fine sediment deposition. Such soils appeared at lower areas where stagnated water remained long after flooding events (ca. one month). The average elevation of these areas was 0.8 m, relative to the lowest stream level. The eutrophic soil subgroup was moderately drained, had mean texture, high sand deposition rates and an average elevation of 2.4 m.

The two soil subgroups showed significant differences for 12 out of the 15 chemical and textural variables (Table 1). In addition to a higher average elevation, the eutrophic subgroup presented higher levels of pH, calcium, sum of bases and sand. The distrophic subgroup presented higher levels of elevation range due to water channels, extractable cation capacity, Al+H, organic matter, clay and silt. We did not find meaningful differences for P, Mg and K levels and according to Tedesco *et al*. (1997), both soils presented high acidity ($pH \leq 5.5$). Because Al levels were imperceptible, those results were not displayed.

Table 1. Topographical and soil variables of the riverside forest of the Rio Botucaraí, Cachoeira do Sul, Southern Brazil. The values are means ± standard deviations of N soil samples collected in the area. Each variable is compared between soil types using two-sample *t* tests (ns = non-significant).

	Distrophic (N = 39)	Eutrophic (N = 61)	*t* tests	P
Average elevation (m)	0.8 ± 1.1 a	2.4 ± 0.8 b	7.33	< 0.001
Elevation range (m)	1.6 ± 0.7 a	1 ± 0.5 b	4.64	< 0.001
pH in H_2O	4.5 ± 0.2 a	4.9 ± 0.1 b	11.24	< 0.001
P – Mehlich (mg.dm^{-3})	6.5 ± 3.6	5.5 ± 0.9	2.00	0.47 ns
K (mg.dm^{-3})	65.8 ±16	62.4 ± 11.1	1.24	0.21 ns
Ca (cmolc.dm^{-3})	8.6 ± 1.8 a	9.5 ± 1.5 b	2.45	0.01
Mg (cmolc.dm^{-3})	3.9 ± 0.9	4.1 ± 0.6	1.35	0.17 ns
Saturation of bases -V (%)	39.7 ± 8.6 a	65.5 ± 9.8 b	13.3	< 0.001
Sum of bases - S (cmolc.dm^{-3})	12.2 ± 3.0 a	14.2 ± 1.9 b	2.11	0.03
CTC (cmolc.dm^{-3})	36.5 ± 8.5 a	22.6 ± 6.1 b	9.48	< 0.001
Al+H (cmolc.dm^{-3})	22 ± 8.1 a	8.2 ± 4.6 b	10.7	< 0.001
Organic matter - O.M. (%)	3.1 ± 0.5 a	2.3 ± 0.5 b	7.42	< 0.001
Sand (%)	34.6 ± 11.5 a	50.4 ± 18.7 b	4.70	< 0.001
Clay (%)	23.7 ± 4.9 a	16.2 ± 4.9 b	7.38	< 0.001
Silt (%)	42 ± 8.8 a	33.3 ± 14.6 b	3.32	< 0.01

Table 2 lists the 30 species surveyed with ecological categories and voucher numbers. The 1,527 individuals surveyed belonged to 24 genera of 16 families. Euphorbiaceae and Myrtaceae were the richest families with five species, followed by Celastraceae, Fabaceae, Rubiaceae, Salicaceae, Sapindaceae and Sapotaceae, with two species each, and the remaining eight families with only one species sampled.

Table 2. Families and tree species surveyed in a riverside forest of the Rio Botucaraí, Cachoeira do Sul, Southern Brazil, with their ecological categories (EC) labeled as P = pioneer, LD = light-demanding and ST = shade-tolerant; T = tall , M = medium and S = small. We registered voucher material and deposited on the ICN herbarium with collect numbers of the first author (see details on methods).

Family/Species	EC	Voucher
Arecaceae		
Syagrus romanzoffiana (Cham.) Glassman	LD-T	-
Celastraceae		
Maytenus dasyclada Mart.	ST-S	541
Maytenus muelleri Schwacke	LD-S	545
Combretaceae		
Terminalia australis Cambess.	P-M	576
Euphorbiaceae		
Gymnanthes concolor Spreng.	ST-S	538
Sapium glandulosum (L.) Morong	P-M	-
Sebastiania brasiliensis Spreng.	LD-M	548

Sebastiania commersoniana (Baill.) L.B.Sm. and Downs	P-M	507
Sebastiania schottiana (Müll. Arg.) Müll. Arg.	P-S	543
Fabaceae		
Apuleia leiocarpa (Vogel) J.F. Macbr.	LD-T	-
Inga vera Willd.	P-S	-
Lamiaceae		
Vitex megapotamica (Spreng.) Moldenke	LD-M	517
Malvaceae		
Luehea divaricata Mart. and Zucc.	P-T	510
Moraceae		
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. and Boer	ST-S	-
Myrsinaceae		
Myrsine lorentziana (Mez) Arechav.	P-M	521
Myrtaceae		
Blepharocalyx salicifolius (Kunth) O. Berg	LD-M	537
Eugenia hiemalis Cambess.	LD-S	479
Eugenia ramboi Legr.	ST-M	147
Eugenia uniflora L.	LD-M	577
Eugenia uruguayensis Cambess.	LD-M	524
Polygonaceae		
Ruprechtia laxiflora Meisn.	LD-T	213
Rubiaceae		
Guettarda uruguensis Cham. & Schltdl.	P-S	405

Psychotria carthagenensis Jacq.	ST-S	550
Salicaceae		
Casearia sylvestris Sw.	LD-M	457
Casearia decandra Jacq.	ST-M	492
Sapindaceae		
Allophylus edulis (A. St-Hil. *et al.*) Radlk.	LD-M	575
Cupania vernalis Cambess.	LD-M	-
Sapotaceae		
Chrysophyllum marginatum (Hook. and Arn.) Radlk.	LD-M	493
Pouteria gardneriana (DC.) Radlk.	P-M	-
Thymelaeaceae		
Daphnopsis racemosa Griseb.	ST-S	-

In the distrophic subgroup, the species with the largest absolute densities were *Sebastiania commersoniana*, *Eugenia hiemalis*, *Eugenia uruguayensis* and *Casearia sylvestris* (Table 3). Notwithstanding 45% of the species presented less than 10 surveyed individuals and 20% had only one. *Sebastiania commersoniana* and *Inga vera* had the highest importance values due to high density or large basal area (Table 3). In the eutrophic subgroup *Sebastiania commersoniana*, *Casearia sylvestris*, *Eugenia uniflora* and *Eugenia hiemalis* had the highest densities and thus these species had the highest importance values (Table 4). Although *Pouteria gerdneriana* and *Inga vera* obtained great basal area these species presented low frequency and an intermediate number of individuals.

Table 3. Structural parameters of distrophic subgroup surveyed in a riverside forest of the Rio Botucaraí, Cachoeira do Sul, Southern Brazil. AD = absolute density, AF = absolute frequency, ADo = absolute dominance, IV = importance value (%), CV = coverage value (%), H = maximum height.

Species	AD (ind.h^{-1})	AF	ADo ($m^2.h^{-1}$)	IV	CV	H
Sebastiania commersoniana	380	37	4.351	38.91	49.06	14
Inga vera	10	8	2.059	8.10	10.14	18
Eugenia uruguayensis	43	23	0.490	7.55	5.54	11
Eugenia hiemalis	47	22	0.433	7.41	5.59	9
Pouteria gardneriana	12	10	1.490	6.81	7.70	13
Casearia sylvestris	34	17	0.280	5.44	3.89	9
Terminalia australis	18	8	1.008	5.32	5.97	10
Eugenia uniflora	17	13	0.116	3.40	1.83	9
Ruprechtia laxiflora	12	8	0.250	2.71	2.06	14
Cupania vernalis	18	8	0.080	2.51	1.75	10
Guettarda uruguensis	10	9	0.046	2.16	0.98	7
Sorocea bonplandii	14	7	0.047	2.03	1.29	8
Allophylus edulis	9	7	0.055	1.80	0.94	7.5
Luehea divaricata	6	5	0.182	1.70	1.29	16
Maytenus muelleri	6	5	0.021	1.21	0.56	7
Myrsine lorentziana	5	4	0.025	1.00	0.50	6.5
Maytenus dasyclada	2	2	0.007	0.46	0.18	6.5
Gymnanthes concolor	2	2	0.006	0.45	0.18	7

Syagrus romanzoffiana	1	1	0.021	0.28	0.17	9
Sapium glandulosum	1	1	0.008	0.24	0.11	6.5
Daphnopsis racemosa	1	1	0.003	0.23	0.09	6.5
Sebastiania schottiana	1	1	0.002	0.22	0.09	4

Table 4. Structural parameters of eutrophic subgroup surveyed in a riverside forest of the Rio Botucaraí, Cachoeira do Sul, Southern Brazil. AD = absolute density, AF = absolute frequency (%), ADo = absolute dominance, IV = importance value (%), CV = coverage value (%), H = maximum height.

Species	AD (ind.h^{-1})	AF	ADo ($m^2.h^{-1}$)	IV	CV	H
Sebastiania commersoniana	343	60	5.006	30.90	37.16	14
Casearia sylvestris	184	50	1.732	16.12	16.49	9
Eugenia uniflora	106	37	0.886	9.86	9.10	9
Eugenia hiemalis	64	32	0.545	6.97	5.53	9
Pouteria gardneriana	23	17	1.438	6.05	6.47	13
Allophylus edulis	49	32	0.394	6.05	4.15	7.5
Inga vera	14	12	1.460	5.26	6.04	18
Luehea divaricata	8	8	0.899	3.31	3.69	16
Eugenia uruguayensis	26	15	0.292	3.18	2.47	11
Ruprechtia laxiflora	9	7	0.762	2.88	3.25	14
Cupania vernalis	14	10	0.049	1.66	0.96	10
Sorocea bonplandii	10	8	0.060	1.33	0.77	8
Daphnopsis racemosa	10	8	0.033	1.27	0.67	6.5

Maytenus muelleri	8	8	0.029	1.19	0.55	7
Terminalia australis	5	3	0.070	0.66	0.67	10
Guettarda uruguensis	4	4	0.031	0.63	0.53	7
Myrcia selloi	4	2	0.030	0.42	0.33	6
Sebastiania schottiana	6	1	0.023	0.38	0.33	4
Maytenus dasyclada	2	2	0.004	0.29	0.42	6.5
Casearia decandra	2	2	0.003	0.29	0.12	6.5
Blepharocalyx salicifolius	1	1	0.042	0.24	0.12	8
Chrysophyllum marginatum	1	1	0.033	0.22	0.21	3
Sebastiania brasiliensis	1	1	0.022	0.19	0.17	7.5
Vitex megapotamica	1	1	0.008	0.16	0.13	7.5
Myrsine lorentziana	1	1	0.002	0.15	0.8	6.5
Apuleia leiocarpa	1	1	0.002	0.14	0.7	4.5
Psychotria carthagenensis	1	1	0.001	0.14	0.7	2.5

Tree density and basal area were not statistically significant between the two subgroups (Table 5). The diameter-class distributions of trees (Figure 2) revealed a typical J distribution, with most individuals concentrated in the first two classes. No significant differences were found ($\chi^2 = 12$; $P = 0.213$) between diameter distributions of the two soil subgroups. The height-class distributions (Figure 3) indicate a relatively low forest, with few trees reaching 14 m in height, most often between 6-8 m, except for some individuals of *Inga vera* and *Luehea divaricata* that were 18 m tall and occurred as emergent trees. *Sebastiania commersoniana*, *Casearia sylvestris* and *Eugenia uniflora* and some shrubs such as *Maytenus muelleri*, *Maytenus dasyclada* and *Daphynopsis racemosa* mainly compose the understorey. Thus, the understorey encompasses many juveniles that may grow and reach the canopy. No differences were found for height-class distribution between the two soil subgroups ($\chi^2 = 42$; $P = 0.227$).

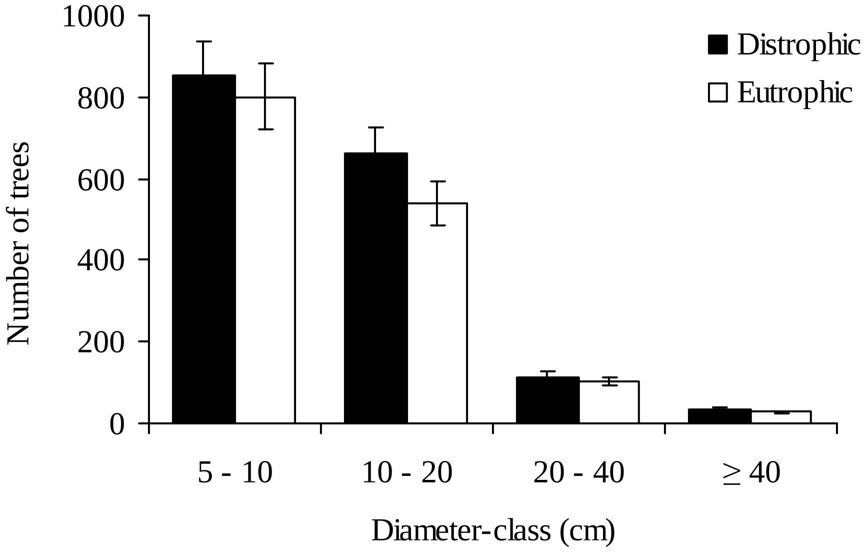

Figure 2. Diameter-class distribution of the trees surveyed in a 1 ha sample site of riverside forest, Cachoeira do Sul, Southern Brazil, arranged into two subgroups. Diameter-classes are for increasing intervals (see methods).

The tree species diversity of the total sample, measured by Shannon's index and Pielou's evenness was 1.995 nats. ind.$^{-1}$ and 0.586, respectively. The Shannon's diversity indices of the two soil subgroups were significantly different ($P < 0.001$) with a lower value for distrophic plots, also associated with lower evenness (0.566) that reflected larger species dominance in those lower areas.

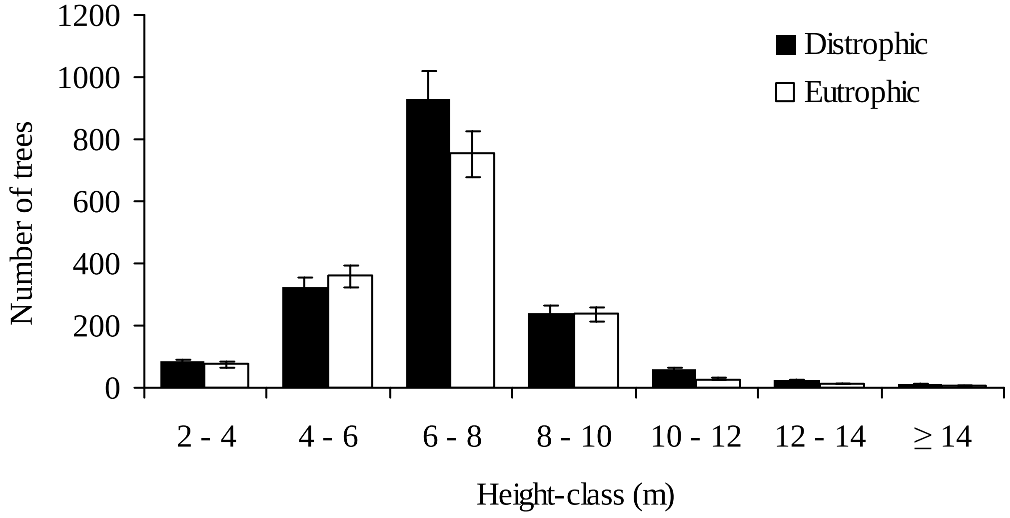

Figure 3. Height-class distribution of the trees surveyed in a 1 ha sample site of riverside forest, Cachoeira do Sul, Southern Brazil, arranged into two subgroups. Height-classes are for 2 m intervals.

Table 5. Number of individuals per area (ind.ha^{-1}), number of species, Shannon diversity index (H') and Pielou evenness (J') in the subsamples and total sample of the riverside forest of Rio Botucaraí, Cachoeira do Sul, Southern Brazil. Different letters after values indicate significant differences in *t* tests (P < 0.001) between pairs of distrophic and eutrophic subsamples.

	Total sample	Distrophic stand	Eutrophic stand	*t* test
Total number of trees (ind.ha^{-1})	1547	1664 ± 870	1472 ± 536	1.45 ns
Basal area (m^2.ha^{-1})	24.85	28.18 ± 18.9	22.72 ± 12.12	1.76 ns
Total number of species, S	30	22	27	
Shannon's diversity, H'(var.)	1.995	1.750 (0.0036) a	2.039(0.0018) b	3.90
Pielou's evenness, J'	0.586	0.566	0.616	

With regard to the ecological categories, 53% of the species were light-demanding and comprised 29% of the individuals (Table 2). Additionally, 36% of the species were pioneers and this group included 69% of all sampled individuals, indicating a majority of early successional species and individuals in the area. Only 11% of the species were shade-tolerant and encompassed 2% of the sampled individuals.

Table 6. Canonical correspondence analysis (CCA) of the 16 surveyed species in 100 contiguous plots of a riverside forest remnant, Cachoeira do Sul, Southern Brazil: matrix of *intraset* correlations between environmental variables and the first two canonical ordination axes thus matrix of weighted correlations between environmental variables.

Variable	Axis 1	Axis 2	Flooding	Al+H	Ca	pH	V	Average elevation
Flooding	0.645	-0.083	-					
Al+H	0.468	0.282	0.621	-				
Ca	-0.248	-0.419	-0.101	-0.092	-			
pH	-0.476	-0.306	-0.698	-0.912	0.175	-		
V	-0.506	-0.387	-0.635	-0.909	0.325	0.898	-	
Average elevation	-0.696	0.067	-0.940	-0.666	0.097	0.732	0.688	-

Figure 4 and 5 show the results of the canonical correspondence analysis (CCA) in two ordination diagrams while Table 6 presents the intraset correlations between environmental variables and the first two ordination axes, in addition to a matrix of weighted correlations between environmental variables. CCA eigenvalues of the two first axes were low: 0.134 and

0.092, respectively, therefore indicating a short gradient, i.e., most species occurred throughout the whole area, varying essentially in their abundances (ter Braack 1995). The cumulative percentage variance accounted for those axes was 7.8% and 5.3% (total accumulation of 13.1%), indicating that a considerable amount of 'noise' still remained unexplained. However, ter Braack (1995) considers low percentage of explained variance as normal in vegetation data, and that this fact does not weaken the significance of species-environment relationships. In fact, the CCA produced high correlations between species and environmental variables (> 0.65) for the first two axes, with significant correlations, yielded by the Monte Carlo permutation test ($P < 0.001$), and carried out for the two first canonical axes.

The first ordination axes were highly correlated, in descending sequence, with average elevation, flooding frequency and saturation of bases (V). For the second axes, the ordination was much less discriminating and only Ca levels were important (Table 6). The weighted correlations between environmental variables showed strong interrelationships, especially between average elevation and flooding frequency (negatively correlated) and between flooding frequency and pH and base saturation and pH, mainly indicating a gradient of poor acid soils, which become rich with the increase of elevation.

The discrimination between distrophic and eutrophic plots in the ordination diagram (Figure 4), represented by different signals enhances the presence of a gradient, from left to right, corresponding to the variation of the average elevation and flooding frequency. The discrimination also shows a high proximity of eutrophic plots with the pH vector, base saturation and Ca levels.

Table 7. Spearman's rank correlation coefficients with respective significance between the species' density and the environmental variables utilized in the canonical correspondence analysis (CCA) for the species surveyed in the riverside forest of Rio Botucaraí, Cachoeira do Sul, Southern Brazil. The species ordered by decreasing correlation with average elevation.

Species	Average elevation	Flooding	pH	Ca	Al+H	V
Casearia sylvestris	0.427^{***}	-0.367^{***}	0.467^{***}	0.276^{**}	-0.462^{***}	0.442^{***}
Cupania vernalis	0.401^{***}	-0.402^{***}	0.077 ns	0.023 ns	-0.049 ns	0.047 ns
Sorocea bonplandii	0.346^{***}	-0.325^{***}	0.064 ns	-0.125 ns	-0.047 ns	0.035 ns
Eugenia uniflora	0.230^{*}	-0.193 ns	0.275^{**}	0.143 ns	-0.293^{**}	0.274^{**}
Allophylus edulis	0.229^{*}	-0.194 ns	0.273^{**}	0.131 ns	-0.236^{*}	0.259^{**}
Luehea divaricata	0.215^{*}	-0.199^{*}	0.029 ns	0.051 ns	0.001 ns	0.018 ns
Daphnopsis racemosa	0.204^{*}	-0.164 ns	0.267^{**}	0.158 ns	-0.253^{*}	0.262^{**}
Ruprechtia laxiflora	0.124 ns	-0.123 ns	-0.029 ns	-0.218^{*}	-0.007 ns	-0.066 ns
Pouteria gardneriana	0.071 ns	-0.044 ns	0.129 ns	-0.078 ns	-0.123 ns	0.067 ns
Inga vera	-0.004 ns	0.042 ns	-0.117 ns	0.087 ns	0.137 ns	-0.107 ns

Eugenia hiemalis	-0.087 ns	0.085 ns	-0.064 ns	-0.200*	0.056 ns	-0.139 ns
Terminalia australis	-0.107 ns	0.056 ns	-0.161 ns	-0.192 ns	0.154 ns	-0.207*
Maytenus muelleri	-0.158 ns	0.153 ns	-0.129 ns	0.015 ns	0.125 ns	-0.103 ns
Eugenia uruguayensis	-0.180 ns	0.151 ns	-0.209*	-0.394***	0.158 ns	-0.282**
Guettarda uruguensis	-0.270**	0.279**	-0.215*	-0.407***	0.230*	-0.300**
Sebastiania commersoniana	-0.515***	0.468***	-0.378***	-0.094 ns	0.375***	-0.405***

*P< 0.05; **P< 0.01; ***P< 0.001; ns, non-significant.

The CCA species ordination (Figure 5) suggests that some species, such as *Sebastiania*

Figure 4. Ordination biplots diagram of plots and environmental variables (vectors) of the first two ordination axes yielded by canonical correspondence anlysis (CCA) based on those species > 10 individuals surveyed on the riverside forest of Rio Botucaraí, Cachoeira do Sul, Southern Brazil.

Schiavini (1997) stated that, in general, there are three topographical sectors in riverine areas that are in fact ecologically different environments: 1) levee, which corresponds to the river margin, close to the stream; 2) depression or intermediate areas, where water stagnates between the levees and the slopes; and 3) slopes or bluffs, located in well-drained areas and without stream influence. The author pointed out there is great species richness in riverine forests due to the diversity of sites that promote differential plant species recruitment. Thus, structural variations in each forest sector would be a consequence of environmental features playing a role in space and time, connected to sedimentation rates, anoxia and nutritional soils status (Oliveira-Filho et al. 1994; Lytle and Poff 2004).

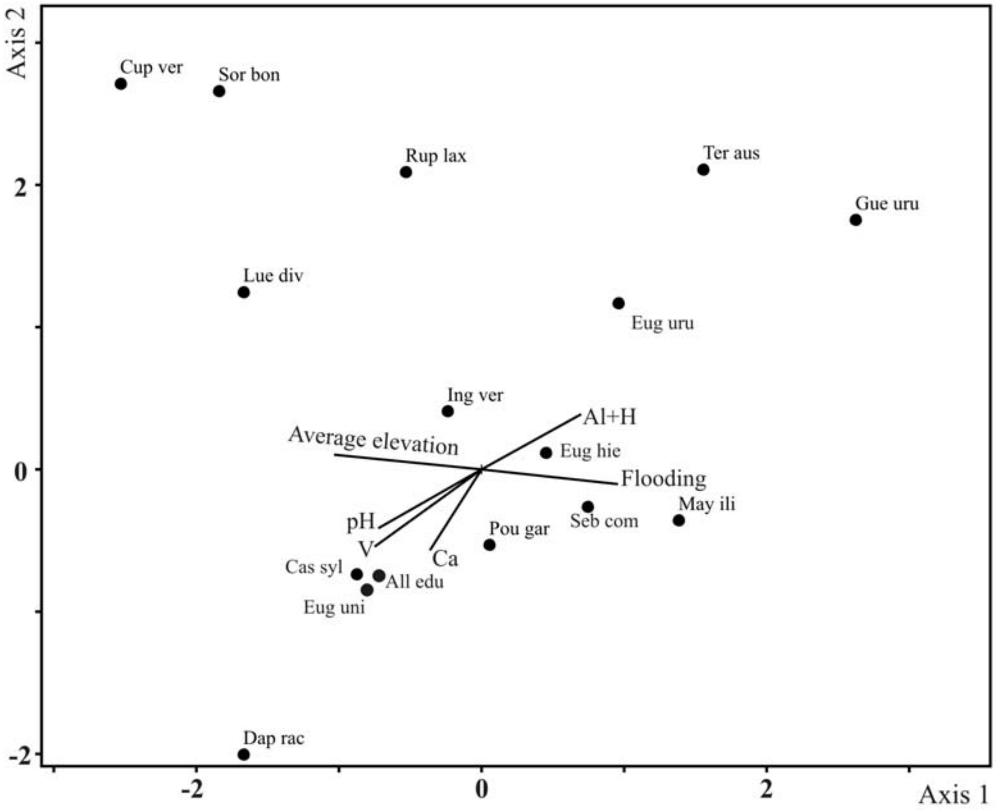

Figure 5. Ordination biplots diagram of species and environmental variables (vectors) of the first two ordination axes yielded by canonical correspondence analysis (CCA) based on those species > 10 individuals surveyed on the riverside forest of Rio Botucaraí, Cachoeira do Sul, Southern Brazil. Species are identified by their abbreviated names (full names in Table 2).

Although the environmental heterogeneity of riverine forests may represent a wide-range of sites for plant recruitment (Tabacchi et al. 1998), flood regimes with long-lasting presence of ground water excess may cause restrictions for the establishment of plants therefore maintaining floodplains with low species richness and diversity (Whittaker 1972). According to this, the low number of species sampled in the current study indicates a local environmental restriction for plant establishment also identified in other studies carried out near the area of this study (Araújo et al. 2004; Budke et al. 2004b). Hence, floods may appear as a regulating factor of chemical and textural soil properties as well as species density.

A clear pattern in nutritional status that emerged from fertility classification of subplots revealed *a posteriori* not only opposite soil responses to the wide range of hydrological regime but also constraining hydrological conditions to the plants, which were ordered according to this gradient. Pélissier et al. (2001) described species optimum and amplitude along the soil gradients of a lowland tropical rainforest, which experience a myriad hydrological and consequently soil properties. According to the authors, these conditions play a key role on species confinement and they support the hypotheses that soil conditions imposed by surface water saturation are more prevalent than water shortage for niche breadth limitation of many tree species.

Concerning our findings, soil properties of the studied stand are a direct consequence of topographic changes and related flooding. Thus, our data also support the hypotheses that flooding regime is a greater determinant of species density and distribution than soil chemical and textural characteristics.

The analysis of the whole sample also revealed low richness and diversity values in comparison to other regional riverside forests. Budke et al. (2004b) described the structure of a riverine forest in the municipality of Santa Maria, central Rio Grande do Sul, and found values of 2.736 nats. ind^{-1} and 0.693 for the Shannon’s diversity index and evenness, respectively.

Although we found statistical differences of diversity between two subgroups, whole sample values suggest high ecological dominance for some species that were favored by flooding events. High densities of pioneers and light-demanding individuals support these findings. Among the species with high IV values, all have the same ecological behavior, i.e. high environmental plasticity and a wide distribution range. The high density of *Sebastiania commersoniana*, a typical pioneer species of flooded areas as well as the presence of *Casearia sylvestris*, *Eugenia uniflora*, *Eugenia hiemalis*, *Inga vera*, *Terminalia australis*, *Pouteria gardneriana* and others, commonly found in riverside forests (Metzger et al. 1997) suggest that the present study area finds itself in an early successional stage.

Oliveira-Filho et al. (1994) stated successional processes vary mainly with local rates of sedimentation, as a direct consequence of flooding events, where forests may appear in a stagnated successional process or in an ongoing pattern of species change. Metzger et al. (1997) states that riverside conditions favor the abundance and frequency of some species such as *Inga vera*, *Ficus insipida*, *Mimosa bimucronata* and *Croton urucurana*, all of them considered to be well-adapted to floods in Southeastern Brazil. In our study, this group encompasses *Sebastiania commersoniana*, *Terminalia australis*, *Inga vera*, *Pouteria gardneriana*, *Guettarda uruguensis*, *Sebastiania schottiana* and *Casearia sylvestris*, which are widely distributed species, occurring especially in riverine forest and are also present in other forest formations (Budke *et al.* 2004b).

The basal area values identified in the present contribution are not different between the soil subgroups and its total value is lower than other similar riverine forests of Rio Jacuí basin. In a minor tributary, Budke et al. (2004b) found basal area of 27 $m^2.ha^{-1}$ and a density of 2,195 $ind.ha^{-1}$ while Araújo et al. (2004) estimated basal area to be 30 $m^2. ha^{-1}$ and a density of 1,832 $ind. ha^{-1}$ for a riparian forest located on the Rio Jacuí. Lower values of biomass and individual abundance in the present study confirm the hypothesis of high environmental restriction, consequently leading to low species richness (Ferreira & Stohlgren 1999).

The different ways species respond to water saturation and related events has been the focus of different works, where variations reflect the complex interactions between species and environmental features (Tabacchi et al. 1998). On the other hand, topographic changes affect spatial distribution patterns in riverside forests, once this feature corresponds to flooding levels and periodicity (Vervuren et al. 2003). In the present study, topography reflects soil fertility and texture levels and leads to a mosaic forest structure. Predominance of *Sebastiania commersoniana*, *Maytenus muelleri* as well as *Terminalia australis*, *Guettarda uruguensis* and the presence of *Sebastiania schottiana* in the lower plots, suggest that these species are tolerant to flooding. On the other hand, high absolute frequency of *Inga vera* and *Pouteria gardneriana*, currently cited as riparian species (Nores et al. 2005) indicates that the whole sampled area is susceptible to flood disturbances, varying in intensity according to the topographic position. The predominance of *Allophylus edulis* and *Sorocea bonplandii* in the high elevation plots reinforces the results obtained by Araújo et al. (2004) for a riverine forest on the Rio Jacuí, municipality of Cachoeira do Sul where there are typical species of non-flooded areas.

In conclusion, it is plausible to support that flooding and soil heterogeneity are playing substantial differences on spatial structuring of this riparian forest. Indeed, environmental variables were ultimately influenced by topographical changes at local scale, as showed by our results. This pattern suggest an argument to hypothesize that in upper sites structural changes are more likely to occur due to species interactions (autogenic succession) than limiting factors as flooding. However, further studies across this environmental gradient are needed especially with population dynamics.

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References

APG II – Angiosperm Phylogeny Group. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. Botanical Journal of the Linnean Society 141: 399 – 436.

Araújo M.M., Longhi S.J., Brena D.A., Barros P.L.C. and Franco S. 2004. Análise de agrupamento de um fragmento de floresta estacional decidual aluvial, Cachoeira do Sul, RS, Brasil. Ciência Florestal 14(1): 133 – 147.

Aveline J. 1944. Regularização dos cursos d'água: os vales e as forças hidroelétricas-açudagem. Tipographya Portela, Cachoeira do Sul.

Bianchini E., Popolo R.S., Dias M.C. and Pimenta J.A. 2003. Diversidade e estrutura de espécies arbóreas em uma área alagável no município de Londrina, Sul do Brasil. Acta Botanica Brasilica 17(3): 405 – 419.

Botrel R.T., Oliveira-Filho A.T., Rodrigues L.A. and Curi N. 2002. Influência do solo e topografia sobre as variações da composição florística e estrutura da comunidade arbóreo-arbustiva de uma floresta estacional semidecidual em Ingaí, MG. Revista Brasileira de Botânica 25(2): 195 – 213.

Budke J.C., Giehl E.L.H., Athayde E.A. and Záchia R.A. 2004a. Distribuição espacial de *Mesadenella cuspidata* (Lindl.) Garay (Orchidaceae) em uma floresta ribeirinha em Santa Maria, RS, Brasil. Acta Botanica Brasilica 18(1): 31 – 35.

Budke J.C., Giehl E.L.H., Athayde E.A., Eisinger S.M. and Záchia R.A. 2004b. Florística e estrutura de uma floresta ribeirinha no arroio Passo das Tropas, Santa Maria, RS, Brasil. Acta Botanica Brasilica 18(3): 581 – 589.

Callegari-Jaques S.M. 2003. Bioestatística: princípios e aplicações. Artmed, Porto Alegre.

Cardoso E. and Schiavini I. 2002. Relação entre distribuição de espécies arbóreas e topografia em um gradiente florestal na Estação Ecológica do Panga (Uberlândia, MG). Revista Brasileira de Botânica 25(3): 277 – 289.

Damasceno-Junior G.A., Semir J., Santos F.A.M. and Leitão-Filho H.F. 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200: 119 – 135.

Embrapa. 1997. Manual de métodos de análises de solo. 2 nd ed. Empresa Brasileira de Pesquisa Agropecuária and Centro Nacional de Pesquisas de Solos, Rio de Janeiro.

Ferreira L.V. and Stohlgren T.J. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. Oecologia 120: 582-587.

Justus J.O., Machado M.L.A. and Franco M.S.M. 1986. Geomorfologia. In: IBGE (ed), Levantamento de Recursos Naturais (33). Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, pp. 313 – 404.

Kandus P. and Malvárez A.I. 1993. Vegetation patterns and change analysis in the lower delta islands of the Parana River (Argentina). Wetlands 24(3): 620 – 632.

Kandus P., Kalesnik F., Borgo L. and Malvárez A.I. 2002. La reserva natural "Isla Botija" en el delta del rio Paraná: analisis de las comunidades de plantas y condicionantes ambientales. Parodiana 12(1-2): 3 – 20.

King R.T. 2003. Sucesion and micro-elevation effects on seedling establishment of *Calophyllum brasiliense* Camb. (Clusiaceae) in an Amazonian river meander forest. Biotropica 35(4): 462 – 471.

Lytle D.A. and Poff N.L. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19(2): 94 – 100.

McCune B. and Mefford M.J. 1997. PC-ORD. Multivariate analysis of ecological data, version 3.0. MjM Software Design, Oregon Glaneden Beach.

Menges E.S. and Waller D.M. 1983. Plant strategies in relation to elevation and light in floodplain herbs. The American Naturalist 122(4): 454 – 473.

Metzger J.P., Bernacci L.C. and Goldenberg R. 1997. Pattern of tree species diversity in riparian forest fragments of different widths (SE Brazil.). Plant Ecology 133: 135 – 152.

Moreno J.A. 1961. Clima do Rio Grande do Sul. Secretaria da Agricultura – Div. Terras e Colonização, Porto Alegre.

Mueller-Dombois D. and Ellenberg H. 1974. Aims and methods of vegetation ecology. John Wiley, New York.

Naiman R.J. and Décamps H. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology and Systematics 28: 621-658.

Nilsson C. and Svedmark M. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. Environmental Management 30(4): 468-480.

Nores M., Cerana M.M. and Serra D.A. 2005. Dispersal of forest birds and trees along the Uruguay River in southern South America. Diversity and Distributions 11: 205 – 217.

Oliveira-Filho A.T., Vilela E.A., Carvalho D.A. and Gavilanes M.L. 1994. Effects of soils and topography on the distribution of tree species in a tropical riverine forest in south-eastern Brazil. Journal of Tropical Ecology 10: 483 – 508.

Oliveira-Filho A.T., Curi N., Vilela E.A. and Carvalho D.A. 2001. Variation in tree community composition and structure with changes in soil properties within a fragment of semideciduous forest in south-eastern Brazil. Edinburgh Journal of Botany 58: 139 – 158.

Pélissier R., Dray S. and Sabatier D. 2001. Within-plot relationships between tree species occurrences and hydrological soil constraints: an example in French Guiana investigated through canonical correlation analysis. Plant Ecology 162: 143 – 156.

Schiavini I. 1997. Environmental characterization and groups of species in gallery forests, In: Proceedings of the International Symposium on Assessment and Monitoring of Forests in Tropical Dry Regions with Special Reference to Gallery Forests, UNB, Brasília. pp. 107 – 113.

Schreiner O.H. 2003. Avaliação da disponibilidade de água na bacia do rio Botucaraí para atender à demanda do arroz irrigado [dissertation]. Canoas: Universidade Luterana do Brasil. 112 p.

Sparovek G., Ranieri S.B.L., Gassner A., Maria I.C., Schung E., Santos R.F. and Joubert A. 2002. A conceptual framework for the definition of the optimal width of riparian forests. Agriculture, Ecosystems and Environment 90: 169 – 175.

Streck E.V., Kämpf N., Dalmolin R.S.D., Klamt E., Nascimento P.C. and Schneider P. 2002. Solos do Rio Grande do Sul. EMATER/RS – UFRGS, Porto Alegre.

Swaine M.D. and Whitmore T.C. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75: 81 – 86.

Tabacchi E., Correll D.L., Hauer R., Pinay G., Planty-Tabacchi A.M. and Wissmar R. 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biology 40: 497 – 516.

Teixeira M.B., Coura-Neto A.B., Patore U. and Rangel Filho A.L.R. 1986. Vegetação; as regiões fitoecológicas, sua natureza, seus recursos econômicos; estudo fitogeográfico. In: IBGE (ed), Levantamento de Recursos Naturais (33). Instituto Brasileiro de Geografia e Estatística, Rio de Janeiro, pp. 541 – 632.

Tedesco M.J., Gianello C., Bissani C.A., Bohnem H. and Volkweiss S.J. 1997. Análise de solo, plantas e outros materiais. UFRGS, Porto Alegre.

Ter Braak C.J.F. 1987. The analysis of vegetation-environment relationship by canonical correspondence analysis. Vegetatio 69: 69 – 77.

Ter Braak C.J.F. 1995. Ordination. In: Jongman R.H.G., ter Braak C.J.F. and van Togeren O.F.R (eds), Data analysis in community and landscape ecology. Cambridge University Press, New York. pp. 91 – 173.

Van den Berg E. and Oliveira-Filho A.T. 1999. Spatial partitioning among tree species within an area of tropical montane gallery forest in south-eastern Brazil. Flora 194: 249 – 266.

Vervuren P.J.A., Blom C.W.P.M. and Kroon H. 2003. Extreme flooding events on the Rhine and survival and distribution of riparian plant species. Journal of Ecology 91: 135 – 146.

Whittaker R.H. 1972. Evolution and measurement of species diversity. Taxon 21(2/3): 213 – 251.

Zar J.H. 1996. Biostatistical analysis. Prentice-Hall, New Jersey.

Capítulo II

Tree community features of two stands of riverine forest under different flooding regimes in Southern Brazil[3]

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Abstract

Two 1 ha plots of a Southern Brazilian subtropical riverine forest, subject to different frequency and duration of floods, were compared to detect the differences in physiognomic structure, tree community composition, richness and diversity. Each plot was made up of 100 contiguous 10 × 10 m subplots, where 3,451 trees with pbh $\geq$ 15 cm were measured and identified. The survey observed 30 tree species, in the frequently flooded plot and 48 in the occasionally flooded plot. A detailed topographical and soil survey was carried out in both plots and indicated that the levels of organic matter and most mineral nutrients were higher in the frequently flooded stand. The forest understory was denser in the occasionally flooded stand which also showed taller emergent trees. Multivariate ordination and grouping techniques showed that the species' abundance distribution was strongly related to the topographical variation. There was a clear pattern of species turnover according to topographic position, indicating that tree species developed different abilities to survive flooding events. As a result, the two plots also differed in their tree frequency per species regeneration, vertical distribution and dispersal guilds. Both species richness and diversity decreased with increasing flood frequency, also showing a patchy distribution within both stands. At a local scale, flooding regimes are regulating the spatial variation of α-diversity by forming different seral stages of predictable species composition. Compared to regularly flooded riverine and floodplain forests, riverine forests, with unpredictable flooding regimes, may show higher diversity at a local scale and more abundant opportunistic species of high environmental plasticity.

Key words: Forest Physiognomy, Indicator Species Analysis, River Overflow, Species Composition, Species Diversity.

Introduction

Riverine systems are transitional areas between land and aquatic ecosystems, arranged in networks across landscapes that include a wide array of socio-economic and biological values. These zones range from the stream channel to the low-high water mark line of the adjoining banks where vegetation may be influenced by either flooding or drought (Naiman and Décamps, 1997; Nilsson and Svedmark, 2002). As non-equilibrium systems providing high environmental heterogeneity, plant communities of river floodplains frequently are among the most productive and diverse in the world, with plant associations of larger complexity than surrounding landscapes (Tockner and Stanford, 2002).

There is a consensus among researchers that overflow is the main environmental variable giving rise to ecological patterns and processes in river floodplains (Bayley, 1995). Running water determines river morphology and is the driving force in the riparian mosaic because of its temporal and spatial variability (Nilsson and Svedmark, 2002). The ecologically most relevant measures of floods are: magnitude, duration, frequency, timing and rate of change (Richter et al., 1996), all of which interact with plant habitat, plant life histories and plant community dynamics (Capon and Brock, 2006). Notwithstanding, a complexity of surrounding features, such as landforms, geomorphologic-sediment structure and climatic conditions, will generate trends that may differ substantially along a river or among rivers, leading to a myriad of ecological responses to recurrent overflow disturbance.

Plant responses to inundation vary from physical to chemical changes (Koslowski, 2002), with soil anoxia and accumulation of toxic elements in the soil as the most significant stress to plant life (Blom and Voesenek, 1996). On the central Amazonian forest floodplain, locally called ‘várzea’, tree species distribution is associated to the gradient of sediment deposition and to the soil texture (Wittmann et al., 2004), which are linked to the flood-level range. The authors pointed out that tree species colonizing seasonal highly inundated areas show specific adaptations to such environmental conditions, e.g. deep primary roots and secondary root layer, newly formed above the fresh deposited sediment, which offers both good mechanical support and better aeration. On the other hand, overflow may benefit some competing species by nutrient accumulation, seed transportation and competitor mortality, especially those classified as stress-tolerant (Grime, 1979).

Concerning the major influence of overflow in river floodplain function and dynamics, Junk et al. (1989) postulated the Flood Pulse Concept which treats rivers and floodplains as unique systems. This model opposed all previous schemes of continuous overflow in explaining biological structuring by addressing discrete annual flood pulses as the primary factor involving changes in biological populations and communities. According to the Flood Pulse Concept, organisms will exhibit adaptations when the flood pulse is seasonally regular (predictable) and, in such case, with sufficient duration. This is the case of tropical river floodplains and some large temperate floodplains for which the concept has been developed (Junk et al., 1989). However, smaller floodplains present more unpredictable floods, which occur in any season, when stream-water level fluctuates as a result of local rainfall on the same river basin, especially in the headwaters. Furthermore, in this situation, both overflow magnitude and rates of change are harnessed to stochastic flood events.

The present contribution, set at a micro-scale perspective, addresses the features of two riverine forests in Southern Brazil, where flood regime is unpredictable and the local overflow magnitude varies, due to different topographic situations. We describe the physiognomic structure; species composition and diversity of an occasionally flooded forest stand and compare it with a nearby frequently flooded stand, previously described by Budke et al. (2007). We addressed the following main questions: (a) Do tree community patterns of physiognomy, species composition and diversity, as well as ecological guilds of regeneration, vertical distribution and dispersal, vary between the frequently and occasionally flooded stands? (b) Can we expect the occurrence of typical species groups in those stands as encountered in large river floodplains with well-regulated inundation pulses?

Methods

Study areas

The study area is a forest remnant of ca. 43 ha situated in the riparian fringes of the Rio Botucaraí near its confluence with the Rio Jacuí (Lat. 30º 01´S, Long. 52º 47´W) (Budke et al., 2007). The headwaters of the river lie in the southernmost extent of the high planes region locally known as Planalto Meridional, which geologically is part of the Serra Geral formation, made up of Cretaceous basalts originating from giant lava flows that covered the sedimentary lowlands of the Paraná Basin (Leinz, 1949). Downstream, at its mid-course the Rio Botucaraí reaches the lowlands and the topography is dominated by recently flood-deposited sediments; meanders and point bars. At its lower course, near the study area, flooding events are enhanced by the confluence with the stronger adjoining stream flow of the Rio Jacuí, therefore promoting a lateral overflow. Furthermore, the flooding tendency of the Rio Botucaraí is also boosted by its gradient factor, from the headwaters (650 m a.s.l) to its discharge (45 m a.s.l.).

The regional climate is moist subtropical, without a regular dry season; the mean annual temperature and rainfall are 19.2 ºC and 1,594 mm.year^{-1}, respectively (IPAGRO, 1982). The predominant soil is a Hydromorphic Planosol, with typical stratified layers of depositional sediments (Streck et al., 2002). Floods in the area are highly unpredictable because there is no one marked seasonal rainy period and rainfall is relatively well distributed throughout the year. As a consequence, floods occur at any time of the year. The duration of overflow periods may vary from some days to a few weeks (Fig. 1).

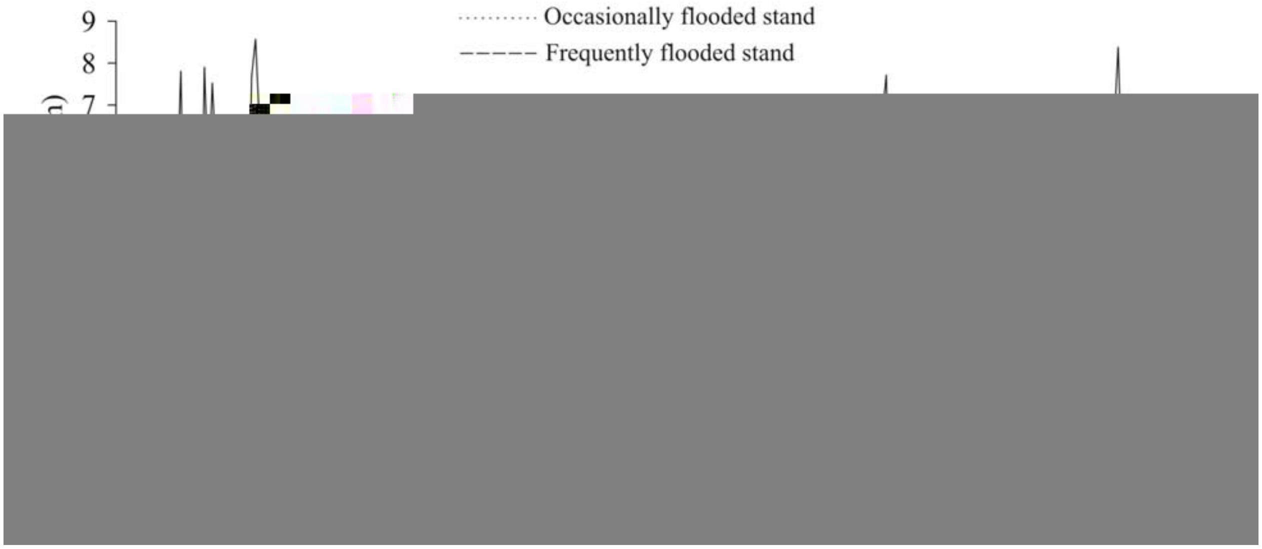

Fig. 1. Mean topography position of two stands of riverine forest in Southern Brazil and hydrological regime between 1981 and 2004 of the Rio Jacuí. Data provided by Agência Nacional de Águas (2006).

Data collection

We carried out a tree survey in two 1 ha plots that represent two different relationships with the river margin and therefore liable to different flooding regimes. We installed the first plot in a low lying area where fine-size sediments and short-lived ponds reflect flooding events of higher frequency and longer duration. The forest structure and relationships with environmental variables of that area were described in Budke et al. (2007). The second plot was set in a more elevated site, ca. 2.5 m above the former. The two plots are ca. 400 m from each other. Both plots were divided into 100 contiguous 10 × 10 m sampling units. All individual living trees, having at least one stem and with perimeter at breast height (pbh) $\geq$ 15 cm were collected. Voucher specimens were deposited in the ICN Herbarium of the Universidade Federal do Rio Grande do Sul (UFRGS).

We carried out a detailed topographic survey of the two plots using a 10 m long water-filled levelling hose, 3/8 in., a tape measurer and a compass, according to Cardoso and Schiavini (2002). The resulting grid of vertical subplots was used to produce contour maps and to obtain two landform variables per subplot: (a) relative elevation to the river and (b) elevation range. These two variables were used to express flooding duration and frequency (Botrel et al., 2002). Hereafter, the two plots or stands are referred

Data analysis

We calculated, for each species, the phytosociological parameters of density, frequency, dominance (derived from tree basal area) and importance values (Mueller-Dombois and Ellenberg, 1974) to describe the tree community structure of the occasionally flooded stand. Phytosociological parameters of the frequently-flooded stand were given in Budke et al. (2007).

Frequency distributions into classes of diameter and height for each stand were prepared and we used two-sample *t*-tests to compare the stands for the mean tree density of each class. Classes of exponentially increasing range were used for diameters to make up for the accentuated decline in tree frequency towards larger diameters (Oliveira-Filho et al., 2001).

In order to answer our questions, we compared the Shannon diversity indices (*H*') of the two stands using bootstrap resampling tests, offered by the software Multiv (Pillar, 2006). Moreover, we prepared a matrix of diversity indices for each 10 × 10 m subplot to enable a topographic assessment of the variations in species diversity within each plot. Successive stepwise multiple regressions were used to identify which variables were significant predictors ($P < 0.05$) of diversity (dependent variable). Independent variables included all chemical and textural soil descriptors, average elevation and elevation range. After a preliminary analysis, insignificant variables were removed and then, dependent and significant non-collinear independent variables (average elevation, silt, sum of bases) were analysed in a multiple linear regression. In addition, linear regression was performed in order to obtain the best predictor of diversity, prior other variables. All regression analyses were conducted using SigmaStat 9.0. We also sought for differences in species richness between the stands using the rarefaction curve technique, which generates expected number of species based on the individuals' density and then provides statistical assumptions to this comparison (Gotelli and Colwell, 2001).

In order to investigate the relationships between frequency and abundance of the species related to topographical features, we performed multivariate ordination techniques. As distributions of species densities generally do not conform to the assumptions of multivariate inferential analysis (Legendre and Andersson, 1999), we chose Principal Coordinates Analysis (PCoA) to obtain orthogonal axes describing the community resemblance among sampling units (subplots). Ordinations were performed in the Multiv statistical package (Pillar, 2006) with Euclidian distance as the resemblance measure.

To verify topographical ranges of the species, which are a direct analysis of association between flooding and species, we used an Indicator Species Analysis – ISA (Dufrêne and Legendre, 1997). As the aim of this analysis was to assess the association between species and topography/flooding, we used a non-hierarchical clustering procedure, *k* means, to produce *k* groups from the mean elevation of the original sampling units (subplots) and then, these resulting groups were performed as the clustering factor in the ISA. As stated by Dufrêne and Legendre (1997), this approach produces an indicator index for a given species which is independent from the relative abundances of other species and, therefore, there is no need to use pseudospecies (Hill, 1979). This analysis was performed with the PC-ORD program (McCunne and Mefford, 1997).

To search for ecological differences among the two plots, we classified the species in ecological groups of regeneration, vertical distribution and dispersal. We defined regeneration based on the categories proposed by Swaine and Whitmore (1988). The two main levels are (a) ‘pioneer’, which includes the species showing an entirely heliophilous life cycle, a seed bank but no juvenile bank, and (b) ‘climax species’, which are those able to germinate and establish themselves under some degree of shade to form a bank of juveniles. The latter was divided into (b1) ‘shade-tolerant’ and (b2) ‘light-demanding climax species’, which are best seen as the two sides of a continuum of solar radiation that is required by the young trees to ‘release’ from the juvenile bank (Oliveira-Filho et al., 1994). We defined the vertical distribution based on the strata commonly reached by the adult individuals: (a) small tree species, (b) medium tree species, and (c) tall tree species (see Oliveira-Filho et al., 1994). The dispersal was: (a) zoochorous, species with animal-mediated dispersal syndrome, (b) anemochorous/hydrochorous, those with mechanisms that facilitate wind-dispersal or flotation, (c) autochorous, those dispersed by free fall or ballistic mechanisms (van der Pijl, 1982). The classification of each species into the ecological groups was based on observations during fieldwork, from 2003 to 2005, and on the scientific literature (Barroso et al., 1999; Budke et al., 2005). In the case of dispersal, we grouped each plant in one or more categories according to the existence of secondary-related dispersal, e.g., *Inga vera*, a primarily endozoochorous species which is also water-dispersed. We also tested the distribution of trees by forming species groups to evaluate the independence of the two plots, using chi-square tests for contingency tables (Zar, 1996).

Results

Soil description and comparison between stands

The chemical and textural analyses of the soils indicated clear differences between the two plots in their soil properties (Table 1). The frequently-flooded stand presented higher levels of P, Ca, Mg, S, V, CEC and organic matter, whereas the occasionally-flooded stand had higher pH and levels of K. With regard to textural variables, no differences were found for sand and silt but, clay contents were higher in the upper sites. As it could be expected, the lower areas had higher cation exchange capacity, bases saturation and sum of bases. There was no difference for potential acidity.

Table 1. Soil variables of the two plots of riverine forest on the Rio Botucaraí, Cachoeira do Sul, in Southern Brazil. Values are means ± standard deviations of 15 soil samples collected at each plot, from a depth of 0-20 cm. Means were compared between plots using two-sample *t* tests (ns = non-significant).

Soil variables	Occasionally flooded stand	Frequently flooded stand	*t*	*P*
pH (H_20)	5.6 ± 0.1	4.7 ± 0.2	3.27	0.001
P – Mehlich (mg.dm^{-3})	5.3 ± 1.2	5.9 ± 2.4	2.05	0.05
K (mg.dm^{-3})	68.4 ± 48.4	48.0 ± 25.3	4.55	0.001
Ca (cmolc.dm^{-3})	3.4 ± 1	9.2 ± 1.7	28.28	0.001
Mg (cmolc.dm^{-3})	1.9 ± 0.4	4.1 ± 0.7	25.93	0.001
Al+H (cmolc.dm^{-3})	12.8 ± 4.7	13.6 ± 9.1	0.77	ns
S (cmolc.dm^{-3})	42.1 ± 10	55.4 ± 15.7	7.14	0.001
CEC (cmolc.dm^{-3})	21.1 ± 5.7	28.1 ± 9.9	6.09	0.001
V (%)	8.4 ± 1.8	13.8 ± 2.4	17.39	0.001
OM (%)	3.1 ± 0.8	4.9 ± 0.6	4.97	0.001
Clay (%)	23.3 ± 4.9	19.1 ± 6.1	5.33	0.001
Sand (%)	42.2 ± 11.8	36.7 ± 13.3	3.07	0.01
Silt (%)	36.5 ± 15.9	44.2 ± 18	3.22	0.01

S = sum of bases, CEC = cation exchange capacity, V = bases saturation, OM = organic matter.

Floristic and structural comparison between stands

The survey of the occasionally flooded stand yielded a total of 1,904 individual trees belonging to 48 species and 21 families (Table 2). This contrasts with the 1,547 trees, 30 species and 16 families registered by Budke et al. (2007) in the frequently flooded stand. The overall basal area of the occasionally flooded stand was 25.95 m^2.ha^{-1}, similar to the 24.85 m^2.ha^{-} registered in the frequently flooded stand. The species with highest absolute densities in the occasionally flooded stand were *Cupania vernalis*, *Luehea divaricata*, *Gymnanthes concolor*, *Sebastiania commersoniana* and *Casearia sylvestris* (Table 2). Notwithstanding, 52% of the species presented less than 10 surveyed individuals. The largest absolute dominances were shown by *Luehea divaricata* (7.5 m^2.ha^{-1}) and *Cupania vernalis* (5.6 m^2.ha^{-1}) reflecting high density or emergent trees with large basal area. The species *Cupania vernalis*, *Luehea divaricata* and *Gymnanthes concolor* had the highest importance values (Table 2). Myrtaceae were the richest family, with nine species, followed by Fabaceae (6), Rubiaceae and Euphorbiaceae (4). Despite its richness, Myrtaceae species appeared mostly at low densities and low basal areas, whereas Sapindaceae, Euphorbiaceae and Malvaceae appeared with large importance values due to high density of some species or large basal area of others.

Table 2. Structural parameters of an occasionally flooded forest stand on the Rio Botucaraí, Cachoeira do Sul, in Southern Brazil. EC = ecological groups, P = pioneer, LD = light-demanding and ST = shade-tolerant; S = small, M = medium, T = tall; Zoo = zoochorous, Ane = anemochorous, Aut = Autochorous, Hyd = hydrochorous; AD = absolute density (ind.ha^{-1}), AF = absolute frequency (%), ADo = absolute dominance (m^2.ha^{-1}), IV = importance value (%).

Species	**EG**	**AD**	**AF**	**ADo**	**IV**
Sapindaceae					
Cupania vernalis Cambess.	LD-M-Zoo	444	91	5.678	56.91
Matayba elaeagnoides Radlk.	LD-T-Zoo	52	32	1.244	11.64
Allophylus edulis (A. St-Hil. et al.) Radlk.	LD-M-Zoo	50	30	0.528	8.52

Euphorbiaceae					
Gymnanthes concolor Spreng.	ST-S-Aut	401	80	1.284	36.3
Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	P-M-Aut/Hyd	131	43	1.424	17.9
Sapium glandulosum (L.) Morong	P-M-Zoo	3	2	0.016	0.48
Sebastiania brasiliensis Spreng.	LD-M-Aut	2	2	0.014	0.42
Malvaceae					
Luehea divaricata Mart. & Zucc.	P-T-Ane	213	72	7.558	49.57
Myrtaceae					
Eugenia hiemalis Cambess.	LD-S-Zoo	34	32	0.222	6.76
Eugenia ramboi D. Legrand	ST-M-Zoo	34	23	0.257	5.74
Eugenia involucrata DC.	LD-M-Zoo	23	17	0.148	3.97
Eugenia schuechiana O. Berg	ST-S-Zoo	17	11	0.073	2.59
Eugenia uruguayensis Cambess.	LD-M-Zoo	13	10	0.110	2.4
Campomanesia xanthocarpa O. Berg	ST-M-Zoo	6	6	0.150	1.67
Myrcia glabra (O.Berg) D.Legrand	ST-M-Zoo	6	6	0.037	1.23
Eugenia uniflora L.	LD-M-Zoo	3	3	0.009	0.58
Myrciaria tenella (DC.) O. Berg	LD-S-Zoo	2	2	0.004	0.38
Salicaceae					
Casearia sylvestris Sw.	LD-M-Zoo	123	56	1.004	17.54
Casearia decandra Jacq.	ST-M-Zoo	22	20	0.110	4.16
Moraceae					
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Boer	ST-S-Zoo	105	58	0.546	15.08
Ficus luschnathiana (Miq.) Miq.	LD-T-Zoo	4	4	0.643	3.2
Fabaceae					

Apuleia leiocarpa (Vogel) J.F. Macbr.	LD-T-Ane	14	11	1.394	7.52
Parapiptadenia rigida (Benth.) Brenan	LD-T-Aut	15	11	1.015	6.12
Inga vera Willd.	LD-M-Zoo/Hyd	23	16	0.289	4.38
Calliandra tweediei Benth.	P-S-Aut	2	2	0.006	0.39
Lonchocarpus nitidus (Vogel) Benth.	LD-M-Ane	1	1	0.051	0.38
Mimosa bimucronata (DC.) Kuntze	P-M-Ane/Hid	1	1	0.037	0.32
Polygonaceae					
Ruprechtia laxiflora Meissn.	LD-T-Ane	44	34	0.301	7.85
Sapotaceae					
Pouteria gardneriana (DC.) Radlk.	P-M-Zoo	8	8	0.458	3.22
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	LD-M-Zoo	10	10	0.106	2.22
Chrysophyllum gonocarpum (Mart. & Eichler) Engl.	ST-M-Zoo	4	4	0.086	1.06
Rubiaceae					
Randia ferox (Cham. & Schltdl.) DC.	ST-M-Zoo	12	11	0.066	2.3
Faramea montevidensis (Cham. & Schltdl.) DC.	ST-S-Zoo	4	4	0.009	0.76
Guettarda uruguensis Cham. & Schltdl.	P-S-Zoo	3	3	0.030	0.66
Chomelia obtusa Cham. & Schltdl.	LD-S-Zoo	2	2	0.009	0.4
Myrsinaceae					
Myrsine lorentziana (Mez) Arechav.	P-M-Zoo	20	12	0.058	2.82
Myrsine coriacea (Sw.) R. Br.	P-M-Zoo	4	3	0.019	0.67
Lamiaceae					
Vitex megapotamica (Spreng.) Moldenke	LD-M-Zoo	6	6	0.294	2.22
Ebenaceae					

Diospyros inconstans Jacq.	LD-M-Zoo	10	10	0.099	2.2
Symplocaceae					
Symplocos uniflora (Pohl) Benth.	LD-M-Zoo	12	9	0.082	2.11
Arecaceae					
Syagrus romanzoffiana (Cham.) Glassman	LD-T-Zoo	4	4	0.314	1.94
Lauraceae					
Nectandra megapotamica (Spreng.) Mez	LD-M-Zoo	4	4	0.033	0.85
Ocotea pulchella (Nees) Mez	LD-M-Zoo	2	2	0.017	0.43
Combretaceae					
Terminalia australis Cambess.	P-M-Ane/Hid	3	1	0.086	0.62
Rhamnaceae					
Scutia buxifolia Reissek	LD-M-Zoo	3	3	0.010	0.59
Celastraceae					
Maytenus dasyclada Mart.	ST-S-Zoo	2	2	0.004	0.38
Annonaceae					
Rollinia salicifolia Schltdl.	LD-M-Zoo	2	2	0.004	0.38
Thymelaeaceae					
Daphnopsis racemosa Griseb.	ST-S-Zoo	1	1	0.001	0.19

The diameter-class distribution of trees produced a typical distribution whose sharp decline towards the larger values was enhanced by an increasing class-range (Fig. 2A). Significant differences in tree density between the stands were found only for the smallest diameter class (5-10 cm), which shows a higher density in the occasionally-flooded stand. The two stands were characterized by a forest of low stature, with most trees between 6 and 8 m in height, but with a few emergent trees being up to 14 m tall. Typical emergent trees were *Inga vera* and *Luehea divaricata*, in the frequently flooded stand, and *Matayba elaeagnoides*, *Luehea divaricata*, *Parapiptadenia rigida* and *Apuleia leiocarpa*, in the occasionally flooded stand. With regard to the height-class distributions (Fig. 2B) differences between the two stands were found for the two smallest classes (2-4 and 4-6 m), again with higher densities in the occasionally-flooded stand. As the minimum size of the survey was defined by diameter and not height, trees of smaller stature are underrepresented and, therefore, their higher density in the occasionally flooded stand would certainly be enhanced if the distributions were purely based on tree heights.

The physiognomic structure of the two stands differs mainly in the higher density of the forest understory in the occasionally flooded plot. Although no significant differences were found for the density of trees of higher stature and larger girth, emergent individuals were visibly larger in the occasionally flooded stand. According to this picture, this stand was not only denser and taller, but also more complex in forest vertical distribution.

Species assemblages and diversity

The first two axes of the PCoA ordination explained *ca*. 66% of the total variation (Axis 1 = 51.9%; Axis 2 = 14.1%) and the sampling units arrangement indicates that there is a strong species gradient in Axis 1, of which the two plots represent overlapping segments (Fig. 3). The gradient starts, at the left side, with a set of sampling units from the occasionally flooded stand and ends at the right side, with a set from the frequently flooded stand, showing some overlapping of both types in the middle.

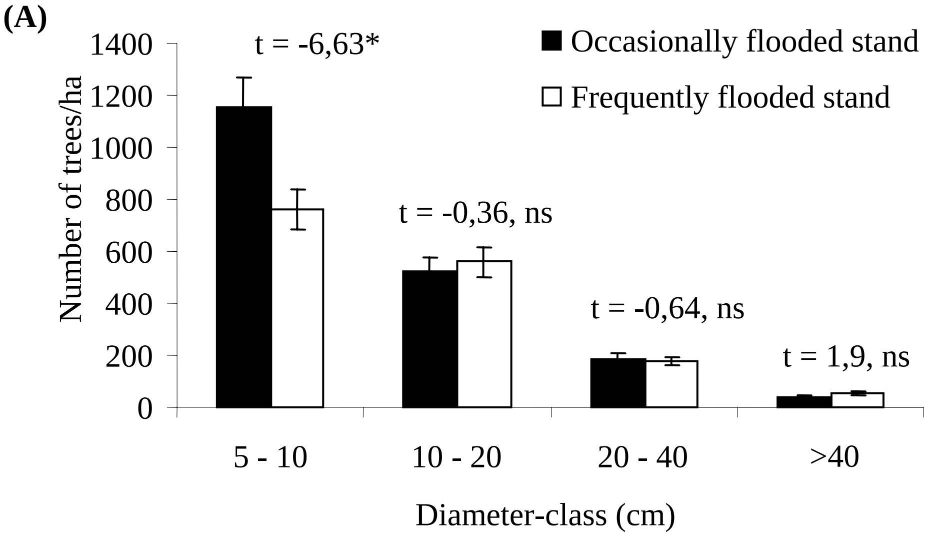

Fig. 2. Diameter-class (A) and height-class (B) distributions of trees with pbh ≥ 15 cm surveyed in two stands of riverine forest on the Rio Botucaraí, in Southern Brazil. Diameter-classes are for increasing intervals (see methods). Bars and ranges are means and 95% confidence intervals of 100 subplots, respectively.

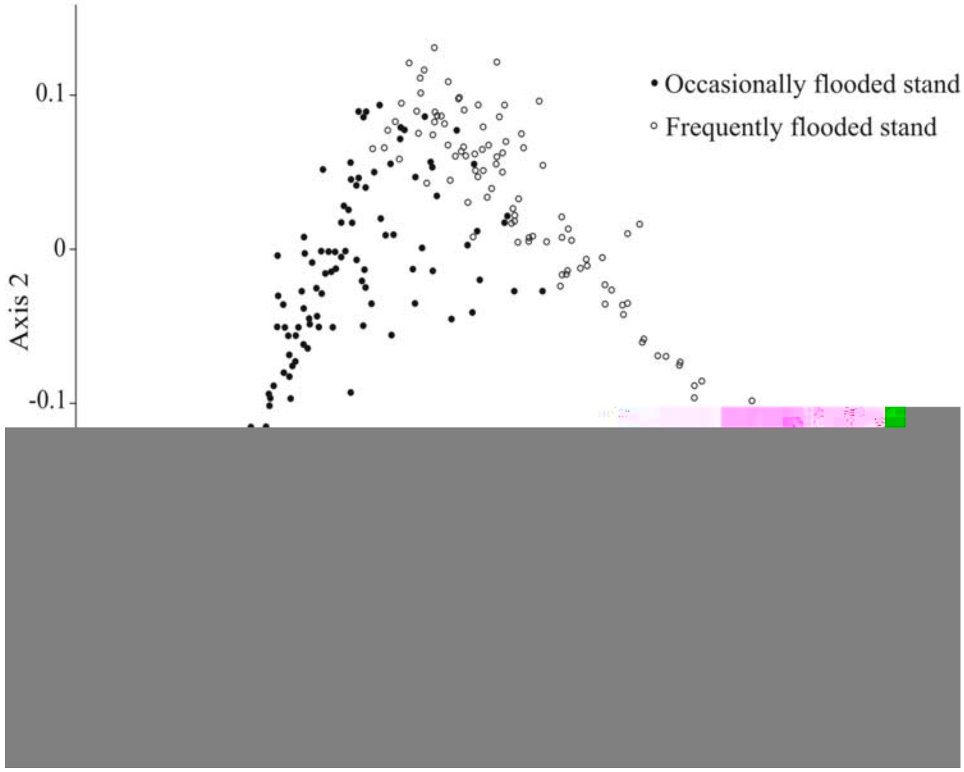

Fig. 3. Ordination of subplots along the first two axes yielded by Principal Coordinate Analysis (PCoA) of the abundance of tree species > 10 individuals, in at least one stand of riverine forest, on the Rio Botucaraí, in Southern Brazil.

This configuration certainly reflects species turnover along a topographic gradient corresponding to different flooding regimes. In fact, the Indicator Species Analysis (Table 3) clearly revealed species distribution according to flooding duration/frequency. Sites of lower to mid elevation had typical riverine species, such as *Eugenia uniflora*, *Sebastiania commersoniana*, *Casearia sylvestris* and *Pouteria gardneriana*. On the other hand, sites of upper to mid elevation showed stronger associations with both species of lower tolerance to floods, such as *Eugenia ramboi* and *Sorocea bonplandii*, and those with a broader distribution in other forest formations, such as *Luehea divaricata*, *Cupania vernalis*, *Matayba elaeagnoides*, *Eugenia involucrata* and *Chrysophyllum marginatum*. Some species did not show any significant association with flooding intensity, although they showed a weak distribution according to a determined site, as occurred with *Diospyros inconstans*, which was not present in lower elevation sites, *Inga vera* and *Allophylus edulis*, which occurred specially in lowland sites.

Table 3. Indicator species analysis (ISA) performed for the species that occurred with 10 or more individuals in at least one of the two stands of riverine forest, on the Rio Botucaraí, in Southern Brazil. OIV = Observed Indicator Value, EIV = Expected Indicator Value.

	Flooding intensity[*]				**OIV**	**EIV**	**P**
Species	**4**	**3**	**2**	**1**			
Lowland to medium sites							
Eugenia uniflora	18	12	8	0	17.9	11.2 ± 2.8	0.03
Casearia sylvestris	21	32	16	3	31.9	20.2 ± 2.7	< 0.01
Sebastiania commersoniana	19	27	24	6	27.3	22.5 ± 2.8	0.06
Pouteria gardneriana	1	12	7	1	12.3	8.3 ± 2.5	0.07
Eugenia schuechiana	0	8	1	1	8	4.2 ± 2	0.05
Medium-high sites							
Eugenia hiemalis	3	17	25	3	24.6	15.6 ± 2.9	0.01
Eugenia uruguayensis	12	2	16	1	15.7	10.3 ± 2.9	0.05
Guettarda uruguensis	0	1	9	2	9.1	5.1 ± 2.1	0.04
Casearia decandra	0	2	9	2	9	5.8 ± 2.2	0.06
Upland sites							
Gymnanthes concolor	0	1	9	46	46.5	14.8 ± 2.8	< 0.01
Cupania vernalis	5	8	11	36	36.3	18.5 ± 2.7	< 0.01
Luehea divaricata	2	12	7	23	23.3	16.2 ± 3.3	0.04

Eugenia ramboi	0	1	0	22	21.9	6.3 ± 2.4	< 0.01
Sorocea bonplandii	7	3	9	22	21.7	13.8 ± 2.8	0.01
Matayba elaeagnoides	0	0	5	19	18.6	8 ± 2.6	< 0.01
Apuleia leiocarpa	0	0	0	13	12.8	4.2 ± 2	< 0.01
Randia ferox	0	0	0	13	12.7	4.2 ± 2	< 0.01
Eugenia involucrata	0	0	2	12	11.6	5.2 ± 2.2	0.02
Chrysophyllum marginatum	0	0	0	11	10.6	4 ± 1.9	0.01
Parapiptadenia rigida	0	0	0	10	9.7	4.2 ± 2	0.02
Without significant association							
Allophylus edulis	12	11	9	5	12	13.2 ± 2.7	Mu7T/TT1 1 Tf12

elevation to the river) and diversity (diversity = 0.98 + 0.125 × relative elevation, $F = 81.68$, $P < 0.001$, $R^2 = 0.29$) with increasing diversity towards more elevated sites (Fig. 5).

The distribution of tree densities among ecological groups differed significantly between the two stands, for all three ecological groups (Table 4). With respect to the regeneration, trees of pioneer species occurred in higher proportions in the frequently flooded stand, while those of shade-tolerant species followed the opposite pattern, with higher proportions in the occasionally flooded stand. Light-demanding trees were equally distributed between the stands. The vertical distribution revealed that trees of understory and emergent species were more frequent in the occasionally flooded stand than in the frequently flooded one. Within dispersal groups, trees of anemochorous and zoochorous species occurred in higher proportions in the frequently flooded stand, while those of autochorous and hidrochorous species occurred at higher frequency in the frequently flooded stand.

Discussion

There is a consensus among researchers that spatial heterogeneity plays a key role in structuring forests worldwide at different spatial scales, with topography representing the best summarizing abiotic variable causing spatial patchiness at a local scale, since it is correlated with a myriad of environmental components, as soil properties and hydrological conditions (Basnet, 1992; Oliveira-Filho et al., 1994a; Ehrenfeld, 1995; Myamoto et al., 2003). In riparian ecosystems, one of the strongest responses of species distribution to topographical features is that related to variations in flooding regimes, resulting in striking variations in species richness and diversity over relatively small physical scales, as those identified for the large Amazonian floodplains (Ferreira and Stohlgren, 1999; Wittmann et al., 2004) and the Pantanal (Damasceno-

Junior et al., 2005). Those ecosystems, however, are characterized by seasonal and regular floods, while those of the present study are highly unpredictable.

Fig. 4. Species rarefaction curves of the two stands of riverine forest, on the Rio Botucaraí, in Southern Brazil.

Floodplains are frequently characterized by particular vegetation formations which include species that are able to survive the floods, either by avoiding or tolerating waterlogging stress (Oliveira-Filho et al., 1994b). Recent studies have described those vegetation formations as early and arrested stages of forest succession characterized by poorly defined canopies and low species diversity (Guilherme et al., 2004; Budke et al., 2007). Some floodplain forests may also include dense monospecific patches of flood-tolerant species, as in the present case, where the patches were formed by *Sebastiania commersoniana*, a typical dweller of riverine forests of Southern Brazil and adjacencies (Bianchini et al., 2003; Budke et al., 2004; Nores et al., 2005).

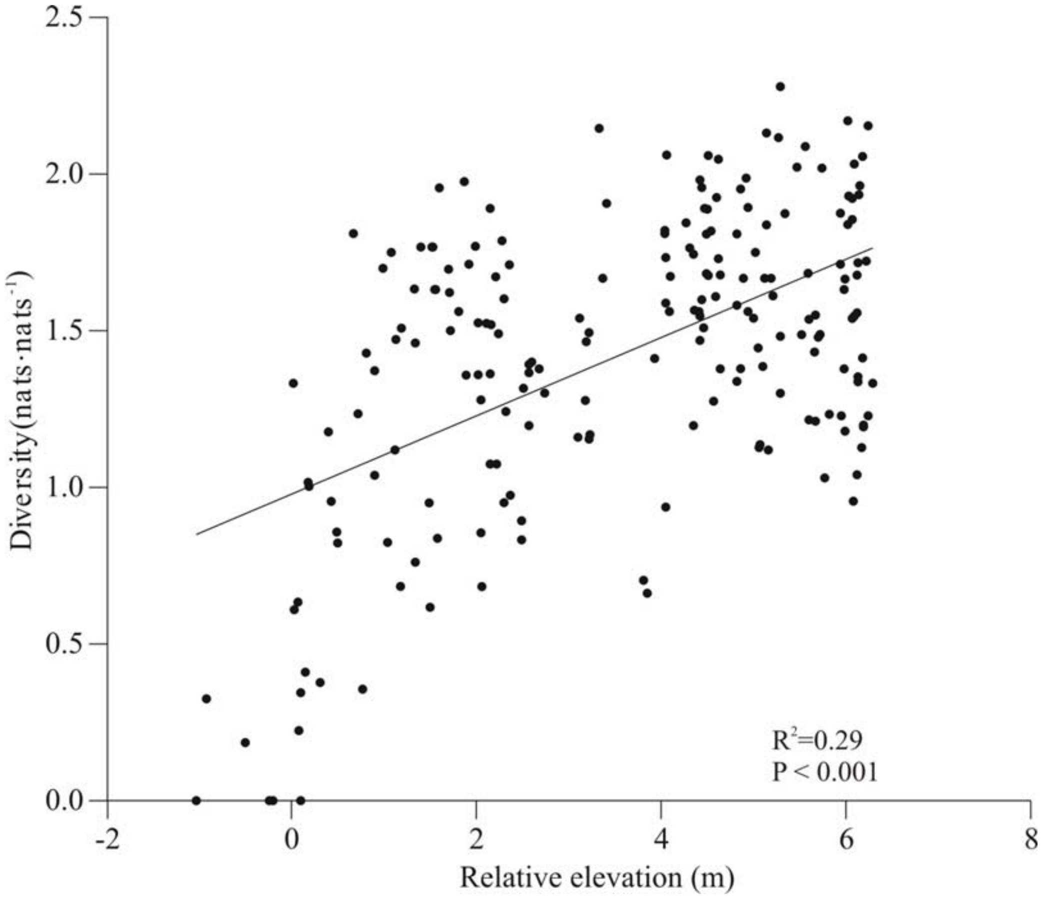

Fig. 5. The relationships between diversity and relative elevation (vertical distance to the river) for the two stands of riverine forest, on the Rio Botucaraí, in Southern Brazil. Diversity = 0.98 + 0.125 × relative elevation.

Table 4. Contingency tables and chi-square tests for the density of trees per species groups of regeneration, vertical distribution and dispersal in two stands of riverine forest, on the Rio Botucaraí, in Southern Brazil. Expected values given within brackets. Dispersal groups also included secondary water dispersal. * = $P < 0.05$; ** = $P < 0.001$.

	Stand		
Ecological categories	**Frequently flooded**	**Occasionally flooded**	**Chi-square test**
Regeneration			
Pioneer	810 (536.1)	386 (659.8)	$\chi^2 = 253.5^{**}$
Light-demanding	694 (716.3)	904 (881.6)	$\chi^2 = 1.2$ ns
Shade-tolerant	43 (294.5)	614 (362.4)	$\chi^2 = 389.4^{**}$
Chi-square tests	$\chi^2 = 355.3^{**}$	$\chi^2 = 288.8^{**}$	$\chi^2 = 644.1^{**}$
Vertical distribution			
Large	37 (171.6)	346 (211.3)	$\chi^2 = 191.3^{**}$
Medium	1318 (1032.3)	985 (211.3)	$\chi^2 = 143.3^{**}$
Small	192 (342.9)	573 (422)	$\chi^2 = 120.5^{**}$
Chi-square tests	$\chi^2 = 255.1^{**}$	$\chi^2 = 204^{**}$	$\chi^2 = 455.1^{**}$
Dispersal			
Anemochorous	36 (138)	272 (169.9)	$\chi^2 = 9.5^{*}$
Autochorous	756 (588.1)	556 (723.8)	$\chi^2 = 87^{**}$
Zoochorous	755 (820.7)	1076 (1010.2)	$\chi^2 = 136.6^{**}$
Chi-square tests	$\chi^2 = 128.5^{**}$	$\chi^2 = 104.6^{**}$	$\chi^2 = 233.1^{**}$

With regard to riverine vegetation, disturbance by floods is frequently perceived as arresting the succession process for long periods (Junk et al., 1989; Capon and Brock, 2006) and local changes in community structure related to environmental variables are associated with allogenic succession (Glenn-Lewin and van der Maarel, 1992). Thus, the structure of each successional stage actually reflects the intensity and frequency of flood-disturbance at each particular site, and the species are arranged according to their capabilities to survive those adverse periods. In our study, ecological traits, represented by the regeneration, vertical distribution and dispersal groups, differed between the stands under different flooding regimes, and this strongly indicates that allogenic forces are driving forest succession, especially in the frequently flooded site. Furthermore, apart from the species composition, most tree community features of the occasionally flooded stand are quite similar to those surrounding mesic non-flooded forests (Lindenmaier & Budke, 2006).

Although forest physiognomic structures differed strikingly between stands, their tree basal area was similar, with major contrasts showing up only among sampling units. The rate of biomass production in long-lasting flooded forests frequently decreases during the inundations as a consequence of unfavourable growth conditions mediated by anoxia (Kozlowski, 2002). Furthermore, the higher levels of organic matter and most mineral nutrients in the frequently flooded stand were probably related to the higher concentration of dead biomass deposits and slow decomposition under the acidic anoxia of water-saturated sites, as demonstrated by Budke et al. (2007) from a micro-scale perspective. Opposing to this, the non-flooded period and the sudden availability of newly deposited nutrients, may represent a very favourable growth-season that largely compensates the previous stagnation. The two systems are, therefore, able to produce and sustain a similar standing biomass, in both plots despite their apparently different growth cycles. On the other hand, minor changes at a local scale, within each plot, may be due to patches of the forest mosaic corresponding to different building phases (Denslow, 1987).

The results of ISA clearly indicated that patterns of plant zonation were a response to flooding tolerance coupled with inter-specific competition. Species which are largely described as tolerant to flooding occurred at higher densities in the frequently flooded stand than in the occasionally flooded one. With the single exception of *Pouteria gardneriana*, which seems to be restricted to low-lying areas (Pennington, 1990), all the following species are indicated as flood-tolerant: *Eugenia uniflora*, *Casearia sylvestris*, *Eugenia schuechiana* and *Sebastiania commersoniana*, also occurring in other forest formations, such as seasonal forests (Jarenkow and Waechter, 2001) and *Araucaria* rain forest, in Southern and South-eastern Brazil (Jarenkow and Budke, 2006). Kubitski (1989) and Parolin et al. (2004) pointed out, that many tree species encountered in Amazonian 'várzea' (floodplain) forests are, in fact, ecotypes originated from surrounding 'terra firme' (upland) forests which are adapted to the floods. Besides, as flood pulses are predictable and regular, the required adaptations may be quite specific, e.g. reproductive trends, which involve both temperature and flood pulsing (Junk et al., 1989). Notwithstanding, in highly variable flood regimes, as in the present case, flexible and opportunistic life history strategies are more likely to develop (Walker et al., 1995). The widespread species found in the floodplain area show several anatomical and physiological responses when submitted to flood conditions (Lobo and Joly, 2000; Medri et al., 2002). This strongly indicates that those species are habitat generalists, that are not primarily adapted to floods, but show instead, high adaptive flexibility that facilitates colonization of those highly disturbed environments.

Topographical changes and related variations in the frequency and duration of inundations are ultimately reflected in local variations of species richness and diversity (α diversity). In the frequently flooded plot, temporary shallow ponds created punctual gaps where α diversity remains near zero. Adjacent marginal spaces are characterized by dense patches of *Sebastiania commersoniana* which also included few individuals of *Casearia sylvestris, Sebastiania schottiana* and *Terminalia australis*, all of which are pioneer tree species. Only in the point bars, where floods are shorter, other tree species appear, so that α diversity is increased (Budke et al., 2007). In the occasionally flooded plot, changes in α diversity indicated a different trend. Depressions and ponds were not present there due to more infrequent and shorter flooding events. In the more elevated sector of the plot, however, dense patches of typical shade-tolerant trees as *Gymnanthes concolor* and *Sorocea bonplandii* reduced local diversity, whereas higher diversity was found at intermediate topographical positions.

As stated by Pollock et al. (1998), microtopographic variation in floodplains give rise to a wide range of spatial variations of the frequency and duration of disturbance by floods. The authors conclude that this spatial heterogeneity increases diversity by creating patches of different serial stages, containing different functional groups. Therefore, the spatial heterogeneity of α diversity across the occasionally flooded stand and the directional increase of α diversity in the frequently flooded stand support, at a local scale, many predictions of the Huston's model (1979, 1994) which related effects of disturbance on plant community responses at the landscape scale to richness and diversity. The existence of an unpredictable flood regime in the whole Rio Botucaraí basin is most probably enhancing spatial diversity at the landscape scale, due to the local variation of intensity of flood-disturbance. At a local scale, topography and related environmental conditions are regulating the spatial variation of α diversity by forming different serial stages of species with predictable ecological traits.

Acknowledgements

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References

Agencia Nacional de Águas. 2006. Sistema de Informações Hidrológicas. URL: www.hidroweb.ana.gov.br.

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.

Basnet, K. 1992. Effects of topography on the pattern of trees in Tabonuco (*Dacryodes excelsa*) dominated rain forest of Puerto Rico. Biotropica 24, 31–42.

Bayley, P.B. 1995. Understanding large river-floodplain ecosystems. BioScience 45, 153–159.

Bianchini, E., Popolo, R.S., Dias, M.C., Pimenta, J.A. 2003. Diversidade e estrutura de espécies arbóreas em uma área alagável no município de Londrina, Sul do Brasil. Acta Bot. Bras. 17, 405–419.

Blom, C.W.P.M., Voesenek, L.A.C.J. 1996. Flooding: the survival strategies of plants. Trends Ecol. Evol. 11, 290–295.

Botrel, R.T., Oliveira-Filho, A.T., Rodrigues, L.A., Curi, N. 2002. Influência do solo e topografia sobre as variações da composição florística e estrutura da comunidade arbóreo-arbustiva de uma floresta estacional semidecidual em Ingaí, MG. Rev. Brasil. Bot. 25, 195–213.

Budke, J.C., Giehl, E.L.H., Athayde, E.A., Eisinger S.M., Záchia, R.A. 2004. Florística e estrutura de uma floresta ribeirinha no arroio Passo das Tropas, Santa Maria, RS, Brasil. Acta Bot. Bras. 18, 581–589.

Budke, J.C., Athayde, E.A. Giehl, E.L.H., Záchia, R.A., Eisinger, S.M. 2005. Composição florística e estratégias de dispersão de espécies lenhosas em uma floresta ribeirinha, arroio Passo das Tropas, Santa Maria, RS, Brasil. Iheringia Bot. 60, 17–24.

Budke, J.C., Jarenkow, J.A., Oliveira-Filho, A.T. 2007. Relationships between tree component structure, topography and soils of a riverine forest, Rio Botucaraí, Southern Brazil. Plant Ecol. 189: 187–200.

Capon, S.J., Brock, M.A. 2006. Flooding, soil seed bank dynamics and vegetation resilience of a hydrologically variable desert floodplain. Freshwat. Biol. 51, 206–223.

Cardoso, E., Schiavini, I. 2002. Relação entre distribuição de espécies arbóreas e topografia em um gradiente florestal na Estação Ecológica do Panga (Uberlândia, MG). Rev. Brasil. Bot. 25, 277–289.

Damasceno-Junior, G.A., Semir, J., Santos, F.A.M., Leitão-Filho, H.F. 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200, 119–135.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. Annu. Rev. Ecol. Syst. 18, 431–451.

Dufrêne, M., Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

Ehrenfeld, J.G. 1995. Microtopography and vegetation in Atlantic White cedar swamps: the effects of natural disturbances. Can. J. Bot. 73, 474–484.

EMBRAPA. 1997. Manual de métodos de análises de solo. Empresa Brasileira de Pesquisa Agropecuária and Centro Nacional de Pesquisas de Solos, Rio de Janeiro.

Ferreira, L.V., Stohlgren, T.J. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. Oecologia 120, 582–587.

Glenn-Lewin, D.C., Maarel, E. van der 1992. Patterns and process of vegetation dynamics. In: Glenn-Lewin, D.C., Peet, R.K., Veblen, T.T. (Eds.), Plant succession, theory and prediction. Chapman and Hall, London, pp. 11–44.

Gotelli, N.J., Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Lett. 4, 379–391.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York.

Guilherme, F.A.G., Oliveira-Filho, A.T., Appolinário, V., Bearzoti, E. 2004. Effects of flooding regime and woody bamboos on tree community dynamics in a section of tropical semideciduous forest in south-eastern Brazil. Plant Ecol. 174, 19–36.

Hill, M.O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101.

Huston, M. 1994. Biological diversity: the coexistence of species in changing landscapes. Cambridge University Press, Cambridge.

IPAGRO 1982. Atlas agroclimático do Rio Grande do Sul. Pallotti, Porto Alegre.

Jarenkow, J.A., Budke, J.C. 2006. Padrões florísticos e análise estrutural de remanescentes florestais com *Araucaria angustifolia* no Brasil. In: Fonseca, C.R., Souza, A.F., Leal-Zanchet, A.M., Dutra, T.L., Backes, A., Ganade, G. (Eds.). Floresta de Araucária: Ecologia, Conservação e Desenvolvimento Sustentável. Ribeirão Preto: Holos (in press).

Jarenkow, J.A., Waechter, J.L. 2001. Composição, estrutura e relações florísticas do componente arbóreo de uma floresta estacional no Rio Grande do Sul, Brasil. Rev. Brasil. Bot. 24, 263–272.

Junk, W.J., Bayley, P.B. and Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. Can. Publ. Fisher. Aquat. Sci. 106, 110–127.

Koslowski, T.T. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. Wetlands 22, 550–561.

Kubitski, K. 1989. The ecogeographical differentiation of Amazonian inundation forests. Plant Syst. Evol. 163, 285–304.

Legendre, P. Andersson, M.J. 1999. Distance-based redundancy analysis: testing multi-species responses in multi-factorial ecological experiments. Ecol. Monogr. 69, 1–24.

Leinz, V. 1949. Contribuição à geologia dos derrames basálticos do Rio Grande do Sul. Bol. Fac. Filos. Cienc. Let. São Paulo 58, 1–55.

Lindenmaier, D.S. & Budke, J.C. 2006. Florística, diversidade e distribuição espacial das espécies arbóreas de uma floresta estacional na bacia do rio Jacuí, sul do Brasil. Pesquisas Bot. 57, 193–216.

Lobo, P.C., Joly, C.A. 2000. Aspectos ecofisiológicos da vegetação de mata ciliar do sudeste do Brasil. In: Rodrigues, R.R., Leitão-Filho, H.F. (Eds.). Matas ciliares, conservação e recuperação. USP/FAPESP, São Paulo, pp. 143–158.

McCune, B., Mefford, M.J. 1997. PC–ORD. Multivariate analysis of ecological data, version 4.36. MjM Software Design, Glaneden Beach.

Medri, M.E., Bianchini, E., Pimenta, J.A., Colli, S., Müller, C. 2002. Estudos sobre tolerância ao alagamento em espécies arbóreas nativas da bacia do rio Tibagi. In: Medri, M.E., Bianchini, E., Shibatta, O.A., Pimenta, J.A. (Eds.). A bacia do rio Tibagi. UEL, Londrina, pp. 133–172.

Mueller-Dombois, D., Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley, New York.

Myamoto, K., Suzuki, E., Kohyama, T., Seino, T., Mirmanto, E., Simbolon, H. 2003. Habitat differentiation among tree species with small-scale variation of humus depth and topography in a tropical health forest of Central Kalimantan, Indonesia. J. Trop. Ecol. 19, 43–54.

Naiman, R.J., Décamps, H. 1997. The ecology of interfaces: riparian zones. Annu. Rev. Ecol. Syst. 28, 621–658.

Nilsson, C., Svedmark, M. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. Environ. Manage. 30, 468–480.

Nores, M., Cerana, M.M., Serra, D.A. 2005. Dispersal of forest birds and trees along the Uruguay River in southern South America. Diversity Distrib. 11, 205–217.

Oliveira-Filho, A.T., Curi, N., Vilela, E.A., Carvalho, D.A. 2001. Variation in tree community composition and structure with changes in soil properties within a fragment of semideciduous forest in south-eastern Brazil. Edinb. J. Bot. 58, 139–158.

Oliveira-Filho, A.T., Vilela, E.A., Carvalho, D.A., Gavilanes, M.L. 1994a. Effects of soils and topography on the distribution of tree species in a tropical riverine forest in south-eastern Brazil. J. Trop. Ecol. 10, 483–508.

Oliveira-Filho, A.T., Vilela, E.A., Gavilanes, M.L., Carvalho, D.A. 1994b. Effect of flooding regime and understory bamboos on the physionomy and tree species composition of a tropical semideciduous forest in south-eastern Brazil. Vegetatio 113, 99–124.

Parolin, P., de Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Piedade, M.T.F. & Junk, W.J. 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. Bot. Rev. 70, 357–380.

Pennington, T.D. 1990. Flora Neotropica 52: Sapotaceae. Hafner Publishing, New York.

Pijl, L.van der. 1982. Principles of dispersal in higher plants. Springer, New York.

Pillar, V.D. 2006. MULTIV. Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling, version 2.3.20. Departamento de Ecologia UFRGS, Porto Alegre.

Pollock, M.M., Naiman, R.J., Hanley, T.A. 1998. Plant species richness in riparian wetlands – a test of biodiversity theory. Ecology 79, 94–105.

Richter, B.D.J.V., Baumgartner, R., Powell, J., Braun, D.P. 1996. A method for assessing hydrologic alteration within ecosystems. Conserv. Biol. 10, 1163–1174.

Streck, E.V., Kämpf, N., Dalmolin, R.S.D., Klamt, E., Nascimento, P.C., Schneider, P. 2002. Solos do Rio Grande do Sul. EMATER/RS and UFRGS, Porto Alegre.

Swaine, M.D., Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75, 81–86.

Tockner, K., Stanford, J.A. 2002. Riverine flood plains: present state and future trends. Environ. Conserv. 29, 308–330.

Walker, K.F., Sheldon, F., Puckridge, J.T. 1995. A perspective on dryland river ecosystems. Regul. Rivers: Res. Manage. 11, 85–104.

Wittmann, F., Junk, W.J., Piedade, M.T.F. 2004. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. For. Ecol. Manage. 196, 199–212.

Zar, J.H. 1996. Biostatistical analysis. Prentice-Hall, New Jersey.

Capítulo III

Distribution of tree species and relationships with spatial and environmental variables in a riverine forest of Southern Brazil[4]

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Abstract

Floods are frequently associated with disturbance in structuring riverine forests and lead to environmental heterogeneity over space and time. We evaluated the distribution of tree species, ecological groups and tree species richness and diversity from the point bar to the slope of a riverside forest in Southern Brazil to analyse the effects of flooding and topography on soil properties and forest structure. A plot of 50 × 200 m divided in five contiguous transects of 10 × 200 m and parallel to the river was installed, where we measured all individual trees with pbh ≥ 15 cm. A detailed topographical and soil survey was carried out across the plot and indicated significant differences in organic matter and most mineral nutrients through the topographical gradient. The 1.229 surveyed individuals belonged to 72 species and 35 families. We used Partial CCA and Species Indicator Analysis to verify the spatial distribution of species. Partial CCA included the species matrix, the 16 variables of the environmental matrix and nine spatial variables from the spatial matrix, whereas Indicator Species Analysis used only flooding as a grouping factor. Both analyses showed that species distribution was strongly related to the flooding gradient, soil properties and also, by space and pure spatial structuring of species and environmental variables (spatial autocorrelation), although a large amount of variation remain unexplained. The ecological groups of stratification, dispersal and requirements for germination indicated slightly differences among frequently, occasional and non-flooded transects. Species richness and diversity were higher at intermediate elevations and it was associated to the increased spatial-temporal environmental heterogeneity. Across the plot, the direct influence of flooding on tree species distribution created a vegetation zonation that is determined by predicted ecological traits.

Key words: Disturbance, Ecological groups, Flooding regime, Partial CCA, Soil properties, Species richness and diversity.

Introduction

Natural disturbances play an important role in structuring plant communities by leading to environmental heterogeneity over space and time at different scales. Several studies have demonstrated the role that disturbance and abiotic stress play over diversity, especially at local-scale (Ferreira & Stohlgren 1999, Weiher 2003). In riparian ecosystems, flooding events are the key factor in shaping community features, either by a positive or a negative effect on the ecosystem's function, according to the timing, frequency and magnitude of such events (Neiff 1990). Long-lasting floods represent a major stress and may result in species-poor plant communities due to restricted productivity in the aquatic phase and high mortality of non-adapted species (Pollock et al. 1998, Guilherme et al. 2004, Wittmann et al. 2004). By other hand, periodic and short floods may contribute to the input of nutrients and then increasing productivity and diversity (Désilets & Houle 2005).

Because magnitude and duration of flooding are directly associated with local relief (e.g. relative elevation, inclination), many studies have investigated the relationships between topography and correlated variables (e.g chemical and textural soil properties, sedimentation rates) on the distribution of plant species and patterns of richness and diversity (Oliveira-Filho et al. 1994, Ferreira 2000, Rosales et al. 2001, Damasceno-Junior et al. 2005, Budke et al. 2007).

In riparian systems with regular or predicted (seasonal) flood events, as Amazonian and Pantanal floodplains in South America, plant species present different strategies to survive the floods, including morphological, anatomical and physiological adaptations and also, phenological timing for both reproductive and vegetative phases. Ferreira et al. (2005) have demonstrated species living in low-lying areas may are ecotypes originated from surrounding non-flooded forests. In contrast, riverine forests with unpredictable flooding pulses frequently are colonized by species of early successional stages of wide geographical distribution (Walker et al. 1995, Budke et al. 2007). Budke et al. (in press) observed that in a small river, where water column oscillate due to a local and concentrated rainy period, the species richness increased along a gradient of frequently to occasionally flooded stands. In this contribution, we focused on species richness and diversity of a topographical sequence with different flooding regimes from a frequently flooded forest transect to a well drained non-flooded forest and we investigated the relationships between tree component structure, species distribution and spatial-environmental variables. We hypothesize that once flooding may gradually affect environmental heterogeneity and that competition may increase at non-flooded areas, richness and diversity will be higher at intermediate elevations and directly associated with increased environmental heterogeneity.

Methods

Study area

The study area is a forest remnant of ca. 20 ha situated in the riparian fringes of the Rio Botucaraí near its confluence with the Rio Jacuí (Lat. 30º 01´S, Long. 52º 47´W) (Budke et al., 2007). The headwaters of the river lie in the southernmost extent of the high planes region locally known as Planalto Meridional, which geologically is part of the Serra Geral formation, made up of Cretaceous basalts originating from giant lava flows that covered the sedimentary lowlands of the Paraná Basin (Leinz, 1949). Downstream, at its mid-course the Rio Botucaraí reaches the lowlands and the topography is dominated by recently flood-deposited sediments - meanders and point bars. At its lower course, near the study area, flooding events are enhanced by the confluence with the stronger adjoining stream flow of the Rio Jacuí, therefore promoting lateral overflow.

The regional climate is moist subtropical, without a regular dry season; the mean annual temperature and rainfall are 19.2 ºC and 1,594 mm.year^{-1}, respectively (IPAGRO, 1982). The predominant soil is a Hydromorphic Planosol, with typical stratified layers of depositional sediments (Streck et al., 2002). Floods in the area are highly unpredictable because there is no one marked seasonal rainy period and rainfall is relatively well distributed throughout the year. As a consequence, floods occur at any time of the year. The duration of overflow periods may vary from some days to a few weeks.

Data collection

We carried out a tree survey in a 1 ha plot installed in a toposequence starting at the river margin, and therefore liable to different flooding regimes. The plot was divided in five 10 x 200 m transects and each transect was subdivided in sampling units of 10 x 10 m. All individual living trees, having at least one stem and with perimeter at breast height (pbh) $\geq$ 15 cm were sampled. Voucher specimens of the different species were collected, prepared and lodged in the Herbarium ICN of the Universidade Federal do Rio Grande do Sul (UFRGS).

We carried out a detailed topographic survey of the transects using a 10 m long water-filled levelling hose, 3/8 in., a tape measurer and a compass, according to Cardoso and Schiavini (2002). The resulting grid of vertical transects was used to produce contour maps and to obtain the relative elevation to the river, which was used to express flooding duration and frequency.

We collected samples of the topsoil (0-20 cm depth) from 15 sites distributed in different positions, in such a way that its overall topographic variation was encompassed. The soil samples were kept in polyethylene bags and taken to the UFRGS Soil Laboratory for chemical and textural analyses. The variables were: pH in water suspension, levels of potassium (K), phosphorus (P), calcium (Ca), magnesium (Mg) and aluminium (Al); potential acidity (Al+H), bases saturation (V), sum of bases (S), cation exchange capacity (CEC), organic matter (OM) and levels of clay, sand and silt. All procedures followed EMBRAPA (1997) protocol. We compared the means of each soil property among transects by using one-way ANOVA (Zar, 1996).

Data analysis

We calculated for each species the phytosociological parameters of density, frequency and dominance (derived from tree basal area) to describe tree community structure (Mueller-Dombois and Ellenberg, 1974). Frequency distributions into classes of diameter for each transect were prepared and we used one-way ANOVA to compare transects. Classes of exponentially increasing range were used for diameters to make up for the accentuated decline in tree frequency towards larger diameters (Oliveira-Filho et al., 2001).

We applied rarefaction curves for each transect in order to analyse the range of species richness within the toposequence. The rarefaction curve technique generates expected number of species based on the individuals' density and then provides statistical assumptions to this comparison (Gotelli and Colwell, 2001). We also compared Shannon diversity indices (*H*') of each transect by bootstrap resampling tests with the software Multiv (Pillar, 2006) and depicted diversity and topography in a regression model.

To verify topographical ranges of the species, we used an Indicator Species Analysis – ISA (Dufrêne and Legendre, 1997), which are a direct analysis of association between flooding and species distribution. As the aim of this analysis was to assess the association between species and topography/flooding we used a non-hierarchical clustering procedure, *k* means, to produce *k* groups from the mean elevation of the original sampling units (subplots) and then, these resulting groups were performed as the clustering factor in the ISA (Dufrêne and Legendre, 1997, Budke et al. in press). The analysis was performed in the PC-Ord program (McCunne and Mefford, 1997).

We partitioned the variance of species distribution over the toposequence accounted by spatial and environmental variables by successive partial Correspondence Canonical Analysis (Borcard et al. 1992). This approach combines three different matrices to decompose all species variation in four components: pure effect of environment, pure effect of spatial pattern, combined variation of environment and spatial pattern and finally, unexplained variation. Species assemblages of a determined position are affected by surrounding sites because of contagious biotic process and, environmental variables used to describe biological processes are also neither randomly nor uniformly spatially-distributed (Legendre 1993). In such case it is necessary to incorporate the spatial structure in the modelling because the independence of observations is not respected (Legendre 1993). The first matrix or species matrix included the abundances of all species with density ≥ 10 individuals. The environmental matrix included initially all chemical and granulometric figures, the topographic variable (average elevation) and an ordinal (ranking) variable, labeled "flooding frequency". We obtained the last variable indirectly from the topographic survey, summarizing flood occurrences and their intensity in each plot (Budke et al. in press). The third matrix or spatial matrix included all terms of a polynomial function of geographical coordinates, i.e., centers of each sampling unit and it was made by adding all terms of a cubic trend surface regression:

$$f(x,y) = x, y, xy, x^2, y^2, x^2y, xy^2, x^3, y^3$$

According to Borcard et al. (1992) this ensure the detection of more complex spatial features as gaps or patches, which require the quadratic and cubic terms of the coordinates and their interactions.

The variance partitioning proceeded in two steps. First, we extracted from each explanatory matrix (environmental variables and spatial variables) all non-significant variables by forward stepwise regression using Monte Carlo permutations (999 permutations, $P < 0.05$) with CANOCO 4.0 (ter Braack & Smilauer 1998) and performed two canonical ordinations that are redundant, in terms of explained variation over the species data due to spatial structuring (Borcard et al. 1992). Then, two partial canonical analysis were carried out (‘environmental’ and ‘spatial’), each of them constrained by one of the sets of explanatory variables, to determine the relative contribution of environmental and spatial variables in accounting for species variation. Final partition is possible by using the sum of all canonical eigenvalues of two canonical ordinations constrained by one set of explanatory variables, and of two partial canonical ordinations, each of them constrained by one set of explanatory variables while controlling for the effect of the others (covariables) (Borcard et al 1992, Titeux et al. 2004).

To search for ecological differences in the toposequence, we classified the species in ecological groups of regeneration, vertical distribution and dispersal. We defined regeneration based on the categories proposed by Swaine and Whitmore (1988). The two main levels are (a) ‘pioneer’, which includes the species showing an entirely heliophilous life cycle, a seed bank but no bank of juveniles, and (b) ‘climax species’, which are those able to germinate and establish under some degree of shade to form a bank of juveniles. The latter was divided into (b1) ‘shade-tolerant’ and (b2) ‘light-demanding climax species’, which are best seen as the two sides of a continuum of solar radiation required by the trees to ‘release’ bank juveniles (Oliveira-Filho et al., 1994).

We defined the vertical distribution based on the strata commonly reached by the adult individuals: (a) small tree species, (b) medium tree species, and (c) tall tree species (see Oliveira-Filho et al., 1994). The dispersal was: (a) zoochorous, species with animal-mediated dispersal syndrome, (b) anemochorous/hydrochorous, those with mechanisms to facilitate wind-dispersal or flotation, (c) autochorous, those dispersed by free fall or ballistic mechanisms (van der Pijl, 1982). The classification of each species into the ecological groups was based on observations during fieldwork, from 2004 to 2005, and on the scientific literature (Barroso et al., 1999; Budke et al., 2005; Budke et al. in press). We tested the distribution of trees into frequency classes according to the ecological group by Kruskal-Wallis tests (Zar, 1996).

Results

River corridor along the studied area has a typical meandering system with well-defined geomorphic features. The lowest sector encompasses the levee and depression, which interact directly with river floods. Next to these sites, we identified the lower-slope, the middle-slope and the ridge, according to the relative elevation to the river channel (Table 1) and these sectors corresponded to our installed transects. The lower slope vegetation is a sharp transition between lowland and upland forests and only large inundation floods this sector, whereas upland sites present slightly differences in vegetation structure due to flood and absence of allied effects. Nevertheless, there is a distinct gradient of organic matter (OM), clay and cation exchangeable capacity, being higher toward upper sites as also showed by potential acidity (Al+H) (Table 1). Furthermore, the variance of some soil variables was quite high and demonstrated the higher heterogeneity through the plot.

Table 1. Soil variables of five transects of riverine forest on the Rio Botucaraí, Southern Brazil. Values are means ± standard deviations, from 0-20 cm depth topsoil samples. Means were compared between transects using ANOVA tests (ns = non-significant).

Soil variables	**Levee**	**Depression**	**L-slope**	**M-slope**	**Ridge**	***F***	***P***
Relative elevation (m)	3.8 ± 0.5 a	5.4 ± 0.7 a	8.5 ± 2.3 b	11.8 ± 3.5 bc	13.6 ± 3.7 c	80.3	< 0.001
pH (H_20)	4.8 ± 0.4	4.7 ± 0.4	4.7 ± 0.4	4.7 ± 0.6	4.7 ± 0.6	0.85	0.93 ns
P – Mehlich (mg.dm^{-3})	7.1 ± 2.1	7.1 ± 2.3	6.3 ± 1.6	6 ± 1.7	5.7 ± 1.4	2.23	0.07 ns
K (mg.dm^{-3})	76.1 ± 12.5	79.6 ± 16.4	89 ± 26.2	94.3 ± 34	87.8 ± 24.1	4.36	0.35 ns
Ca (cmolc.dm^{-3})	6.2 ± 4.3	6.8 ± 4.4	7 ± 4.7	6.1 ± 4	5.7 ± 3.7	3.19	0.52 ns
Mg (cmolc.dm^{-3})	1.5± 0.7	1.6 ± 0.7	1.5 ± 0.7	1.5 ± 0.6	1.4 ± 0.5	0.36	0.98 ns
Al+H (cmolc.dm^{-3})	6.6 ± 3.1 a	7.1 ± 3 ab	8.5 ± 4 ab	9.6 ± 5.5 ab	10 ± 4.2 b	9.76	0.04
S (cmolc.dm^{-3})	8 ± 4.8	8.7 ± 5.1	8.1 ± 4.6	8.4 ± 5.1	7.4 ± 4.1	2.77	0.59 ns
CEC (cmolc.dm^{-3})	15.2 ± 4.8	16.2 ± 3.8	17.1 ± 3.3	17.9 ± 4.3	17.3 ± 3.4	1.45	0.22 ns
V (%)	55.7 ± 17.1	49.7 ± 20.2	45.9 ± 24.6	45.5 ± 23.6	41.8 ± 20.7	4.06	0.39 ns
OM (%)	2.6 ± 1.1 a	2.8 ± 1 a	3.2 ± 1 ab	3.7 ± 1.1 b	3.8 ± 0.8 b	22.9	< 0.001
Clay (%)	13.7 ± 2.4 a	15.4 ± 3.3 ab	15.8 ± 2.8 ab	16 ± 2.1 b	15.5 ± 1.7 ab	2.49	0.04
Sand (%)	20 ± 7.4	23.1 ± 2.2	24.2 ± 10.1	22.3 ± 7.5	22.3 ± 6.2	8.91	0.06 ns
Silt (%)	64.2 ± 10.9	60.4 ± 14	59.8 ± 12.9	62 ± 9.1	62 ± 7.2	4.91	0.29 ns

Table 2. Structural parameters of a riverine forest on the Rio Botucaraí, Southern Brazil. AF = absolute frequency (%), ADo = absolute dominance ($m^2.ha^{-1}$), EG = ecological groups, P = pioneer, Ld = light-demanding and St = shade-tolerant; S = small, M = medium, T = tall; Zoo-Z = zoochorous, Ane = anemochorous, Aut = Autochorous, Hyd = Hydrochorous.

Species	**Density (ind.ha-1)**					**AF**	**ADo**	**EG**
	Levee	depression	L-slope	M-slope	Ridge			
Fabaceae								
Apuleia leiocarpa (Vogel) J.F.Macbr.	5	5	8	9	3	24	3.448	Ld-T-Ane
Parapiptadenia rigida (Benth.) Brenan	3	1	2	4	9	17	0.585	Ld-T-Aut
Myrocarpus frondosus Allemão	0	10	11	3	2	8	0.284	Ld-T-Ane
Machaerium paraguariense Hassl.	3	2	4	2	2	12	0.432	Ld-M-Ane
Enterolobium contortisiliquum (Vel.) Morong	2	1	0	0	1	4	0.562	Ld-T-Zoo
Dalbergia frutescens (Vell.) Britton	0	0	1	4	0	5	0.030	Ld-M-Ane
Lonchocarpus nitidus (Vogel) Benth.	1	0	1	2	0	4	0.021	Ld-M-Ane
Lonchocarpus campestris Mart. ex Benth.	0	0	1	2	0	3	0.065	Ld-M-Ane
Inga vera Willd.	1	0	2	0	0	3	0.052	Ld-M-Z/Hyd
Erythrina falcata Benth.	0	0	1	0	0	1	0.155	Ld-T-Ane
Calliandra tweediei Benth.	0	1	0	0	0	1	0.002	Ld-M-Aut

Euphorbiaceae								
Gymnanthes concolor Spreng.	22	14	15	34	15	54	0.378	St-S-Aut
Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	31	19	2	2	1	25	1.153	P-M-Aut
Sebastiania brasiliensis Spreng.	7	7	3	14	9	30	0.874	Ld-M-Aut
Myrtaceae								
Eugenia uniflora L.	36	6	0	0	0	17	0.362	Ld-M-Zoo
Eugenia uruguayensis Cambess.	31	11	0	0	0	15	0.278	Ld-M-Zoo
Myrciaria tenella (DC.) O.Berg	19	2	0	0	0	12	0.164	Ld-S-Zoo
Eugenia involucrata DC.	0	2	3	6	5	11	0.270	Ld-M-Zoo
Eugenia ramboi D.Legrand	2	5	3	3	0	10	0.156	St-M-Zoo
Campomanesia xanthocarpa O.Berg	1	1	2	4	3	10	0.163	St-M-Zoo
Myrcianthes pungens O.Berg	6	3	2	1	1	7	0.136	Ld-M-Zoo
Myrcia glabra (O.Berg) D.Legrand	1	2	2	5	0	8	0.118	St-M-Zoo
Eugenia hiemalis Cambess.	3	1	2	0	2	8	0.058	Ld-S-Zoo
Calyptranthes conccina DC.	1	0	1	0	0	2	0.015	St-M-Zoo
Myrcia multiflora (Lam.) DC.	1	0	0	0	0	1	0.004	Ld-M-Zoo
Sapotaceae								

Chrysophyllum marginatum (Hook. & Arn.) Radlk.	14	6	18	20	13	45	1.634	Ld-M-Zoo
Pouteria gardneriana (DC.) Radlk.	7	3	4	1	0	12	0.901	P-M-Zoo
Sideroxylon obtusifolium (Roem. & Schult.) T.D.Penn.	0	1	1	1	0	3	0.302	Ld-T-Zoo
Chrysophyllum gonocarpum (Mart. & Eichler) Engl.	0	0	3	1	1	5	0.086	St-M-Zoo
Rubiaceae								
Guettarda uruguensis Cham. & Schltdl.	29	16	6	4	4	39	0.304	P-S-Zoo
Chomelia obtusa Cham. & Schltdl.	3	5	7	24	17	37	0.362	Ld-S-Zoo
Faramea montevidensis (Cham. & Schltdl.) DC.	0	1	8	1	0	8	0.022	St-S-Zoo
Randia ferox (Cham. & Schltdl.) DC.	4	1	1	0	1	7	0.055	St-M-Zoo
Salicaceae								
Casearia sylvestris Sw.	21	17	21	19	7	45	1.620	Ld-M-Zoo
Casearia decandra Jacq.	1	2	2	0	0	5	0.078	St-M-Zoo
Xylosma sp.	0	0	0	1	0	1	0.028	Ld-M-Zoo
Sapindaceae								
Matayba elaeagnoides Radlk.	9	11	3	12	0	18	1.573	Ld-T-Zoo
Allophylus edulis (A. St-Hil. et al.) Radlk.	5	2	5	6	1	15	0.241	Ld-M-Zoo
Cupania vernalis Cambess.	0	0	5	3	4	10	0.346	Ld-M-Zoo

Moraceae							
Sorocea bonplandii (Baill.) W.C. Burger et al.	7	3	13	22	12	37	0.412	St-S-Zoo
Ficus luschnathiana (Miq.) Miq.	3	0	2	0	2	7	1.464	Ld-T-Zoo
Boraginaceae								
Cordia americana (L.) Gottschling & J.E.Mill.	8	7	12	14	19	39	1.957	Ld-T-Ane
Polygonaceae								
Ruprechtia laxiflora Meisn.	14	0	5	6	3	22	0.856	Ld-T-Ane
Coccoloba cordata Cham.	1	0	0	0	0	1	0.003	P-M-Zoo
Annonaceae								
Rollinia salicifolia Schltdl.	3	7	4	8	14	27	0.507	Ld-M-Zoo
Lauraceae								
Ocotea pulchella (Nees) Mez	5	1	6	5	2	14	0.413	Ld-M-Zoo
Ocotea puberula (Rich.) Nees	0	0	3	2	4	7	0.552	Ld-M-Zoo
Myrsinaceae								
Myrsine coriacea (Sw.) R. Br.	1	3	1	2	1	7	0.564	P-M-Zoo
Myrsine lorentziana (Mez) Arechav.	0	2	0	7	6	9	0.069	P-M-Zoo
Myrsine loefgrenii (Mez) Imkhan.	0	0	1	0	0	1	0.006	P-M-Zoo
Malvaceae								

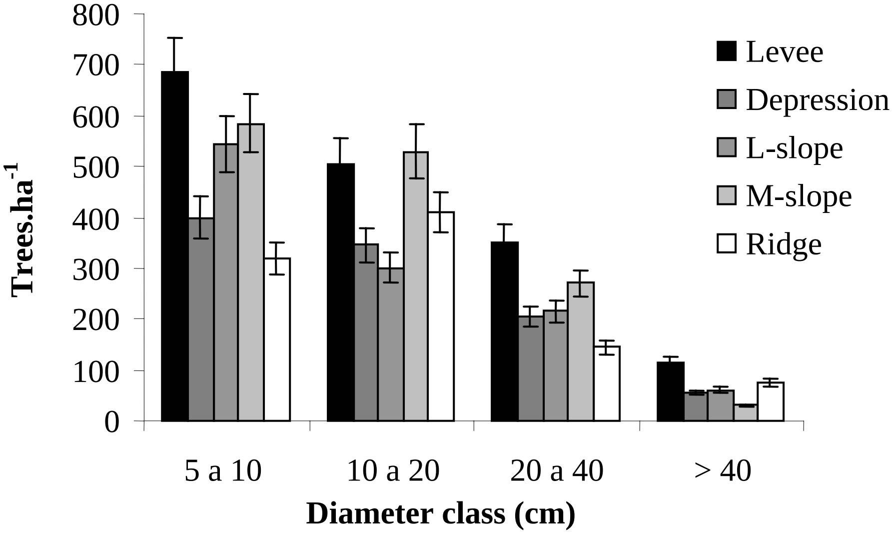
Luehea divaricata Mart. & Zucc.	3	1	5	6	2	15	0.635	P-T-Ane
Meliaceae								
Trichilia elegans A.Juss.	3	4	3	4	7	16	0.088	St-S-Zoo
Trichilia claussenii DC.	0	1	1	0	1	3	0.041	St-M-Zoo
Loganiaceae								
Strychnos brasiliensis (Spreng.) Mart.	3	4	5	3	4	12	0.098	Ld-M-Zoo
Arecaceae								
Syagrus romanzoffiana (Cham.) Glassman	1	1	4	1	1	7	0.447	Ld-T-Zoo
Phytolaccaceae								
Phytolacca dioica L.	0	0	0	0	2	2	0.616	Ld-T-Zoo
Cannabaceae								
Celtis iguanaea (Jacq.) Sarg.	0	1	3	5	1	10	0.064	Ld-M-Zoo
Rhamnaceae								
Scutia buxifolia Reissek	3	0	0	1	0	4	0.299	Ld-M-Zoo
Bignoniaceae								
Tabebuia heptaphylla (Vell.) Toledo	1	0	0	1	0	2	0.385	Ld-T-Ane
Lamiaceae								
Vitex megapotamica (Spreng.) Moldenke	0	4	1	0	1	5	0.145	Ld-M-Zoo

Solanaceae								
Solanum sanctaecatharinae Dunal	0	0	0	3	2	5	0.110	Ld-M-Zoo
Anacardiaceae								
Lithraea brasiliensis Marchand	0	0	0	2	2	4	0.165	Ld-M-Zoo
Ebenaceae								
Diospyros inconstans Jacq.	1	1	1	0	1	4	0.097	Ld-M-Zoo
Celastraceae								
Maytenus dasyclada Mart.	3	2	1	0	0	4	0.025	St-S-Zoo
Rosaceae								
Prunus myrtifolia (L.) Urb.	0	1	0	1	0	2	0.074	Ld-M-Zoo
Asteraceae								
Gochnatia polymorpha (Lam.) Cabrera	0	0	0	0	1	1	0.074	Ld-M-Ane
Symplocaceae								
Symplocos lanceolata (Mart.) DC.	0	0	0	1	1	2	0.017	Ld-M-Zoo
Rutaceae								
Zanthoxylum rhoifolium Lam.	0	0	2	0	0	1	0.031	Ld-M-Zoo
Verbenacease								
Cytharexylum montevidense (Spreng.) Moldenke	0	0	0	1	0	1	0.013	Ld-T-Zoo

Simaroubaceae								
Picrasma crenata (Vell.) Engl.	1	0	0	0	0	1	0.005	St-M-Zoo
Combretaceae								
Terminalia australis Cambess.	0	0	1	0	0	1	0.004	P-M-Ane
Erythroxylaceae								
Erythroxylum myrsinites Mart.	1	0	0	0	0	1	0.004	Ld-M-Zoo

The field inventory yielded a total of 1,229 individuals belonging to 72 species and 35 families, from which, Myrtaceae and Fabaceae were the richest families with 11 species, followed by Rubiaceae and Sapotaceae with four species (Table 2). Although Myrtaceae and Fabaceae presented highest richness both families appeared generally with low density or basal area. The stand was characterized by a forest of low stature with most individuals between 5 and 7 m tall and few emergent trees reaching up 15 m. The diameter-class distribution of trees revealed typical inverted-J distribution, with most individuals situated in the first two classes (Fig. 1). Across the toposequence, higher density was found near the river (Levee) followed by lower density values in the depression and again, an increased density through lower and middle slope. By other hand, the ridgetop transect presented the lowest density but an increased basal area (Table 3) and several trees with diameter > 40 cm. Vertical distribution of trees also showed the predominance of medium individuals, followed by a decreased proportion of small and emergent trees (Fig. 2 A).

The proportion of light-demanding trees was higher towards the upper sites (Fig. 2 B). Pioneer trees presented an opposite pattern, being more abundant in low sites. Shade-tolerant trees also showed an increased density at upper sites where flooding is restrict or absent. Within the dispersal groups, zoochorous trees presented higher proportion in all transects. Autochorous and hydrochorous trees decreased toward the ridgetop, whereas anemochorous trees followed the inverse pattern (Fig. 2 C). These structural patterns shaped the physiognomic features of different sectors that varied according to the toposequence and consequently in flooding regime. The depression sector presented lower density, basal area and also low tree diameters, whereas the levee portion presented high density and basal area.


800
700
600
500
400
300
200
100
0
Trees.ha-1
Levee
Depression
L-slope
M-slope
Ridge
5 a 10
10 a 20
20 a 40
> 40
Diameter class (cm)

Ridge	950 ± 294 b	28.2 ± 19.4 b	7 ± 2.4 b	17.27 ± 15.55
ANOVA	$F = 10.7^*$	$F = 12.9^*$	$F = 30.5^*$	$F = 3.5^*$

$^*P < 0.001$

Table 4. Indicator species analysis (ISA) performed for the species with density ≥ 10 in the plot, Rio Botucaraí, Southern Brazil. IV = Observed Indicator Value, ^{ex}IV = Expected Indicator Value.

	Relative elevation							
Species	**1**	**2**	**3**	**4**	**5**	**IV**	**^{ex}IV**	**P**
Lowland to medium sites								
Eugenia uniflora	51	1	0	0	0	51.5	9.7 ± 3.7	< 0.001
Myrciaria tenella	48	0	0	0	0	48	8.2 ± 3.5	< 0.001
Eugenia uruguayensis	42	2	0	0	0	41.6	9.1 ± 3.7	< 0.001
Sebastiania commersoniana	36	11	1	0	0	35.9	12 ± 4.1	< 0.001
Guettarda uruguensis	30	15	1	1	5	30.3	14.9 ± 3.9	< 0.001
Pouteria gardneriana	15	4	1	0	1	14.8	7.7 ± 3.3	0.03
Matayba elaeagnoides	9	2	27	0	0	26.6	10.2 ± 4	< 0.001
Myrcia glabra	1	0	24	0	0	24.3	6.9 ± 3.5	< 0.001
Eugenia ramboi	0	5	21	0	0	20.6	7.6 ± 3.5	< 0.001
Myrsine lorentziana	0	1	18	4	0	17.6	7.1 ± 3.3	0.01
Apuleia leiocarpa	6	3	17	1	3	17.4	11.3 ± 3.7	0.06
Allophylus edulis	2	3	17	1	1	16.7	8.9 ± 3.5	0.04
Strychnos brasiliensis	1	2	16	1	0	16.1	8.1 ± 3.6	0.03
Faramea montevidensis	0	9	12	0	0	12	6.8 ± 3.2	0.08
Medium to upland sites								

Chomelia obtusa	1	2	5	11	44	43.6	14.3 ± 3.8	< 0.001
Cordia americana	2	1	1	21	38	38.1	14.9 ± 3.7	< 0.001
Chrysophyllum marginatum	6	6	9	6	22	22.2	15.9 ± 3.5	0.05
Sorocea bonplandii	2	3	20	22	2	21.8	14.3 ± 3.8	0.04
Parapiptadenia rigida	1	1	0	7	17	17.3	9.2 ± 3.2	0.02
Cupania vernalis	0	0	1	14	4	14	7.2 ± 3.1	0.04
Celtis ehrenbergiana	0	0	1	12	5	12.2	7.2 ± 3.3	0.06
Without significant association								
Gymnanthes concolor	15	5	21	5	14	20.7	17.7 ± 3.8	0.19
Casearia sylvestris	12	9	11	8	5	12.1	16 ± 3.5	0.90
Rollinia salicifolia	1	3	3	15	11	15.5	11.9 ± 3.6	0.14
Ruprechtia laxiflora	14	1	11	2	0	13.6	10.9 ± 3.6	0.19
Trichillia elegans	0	2	1	10	7	10.4	9.2 ± 3.6	0.27
Sebastiania brasiliensis	4	4	6	8	10	10.1	12.6 ± 3.6	0.77
Eugenia involucrata	0	1	10	10	0	10	7.9 ± 3.6	0.21
Luehea divaricata	2	1	8	2	6	8.5	8.7 ± 3.4	0.41
Machaerium paraguariense	2	1	0	5	8	8.2	7.9 ± 3.5	0.33
Ocotea pulchella	3	2	8	5	0	7.6	8.8 ± 3.5	0.54
Campomanesia xanthocarpa	0	1	8	1	4	7.6	7.3 ± 3.1	0.38
Myrocarpus frondosus	0	5	0	7	1	7.4	7 ± 3.5	0.35
Myrcianthes pungens	5	1	0	2	1	5	6.7 ± 3.3	0.64

Species distribution across the topographic gradient is presented in Table 4, according to the Indicator Species Analysis. Some species were clearly distributed from lowland to medium sites as *Eugenia uniflora*, *Myrciaria tenella*, *Eugenia uruguayensis*, whereas others were restrict to upland areas as *Chomelia obtusa* and *Cordia americana*. Many species did not show a specific site distribution and occurred over a wide distribution range.

The relative elevation of each transect reflects the pattern of flooding frequency and duration in each site, then spatial aggregation of trees may indicate preferences or restriction on the establishment of some species. Typical riverine species appeared near the river margin as *Pouteria gardneriana*, *Guettarda uruguensis* and others (Table 4), whereas typical species of well-drained forests as *Sorocea bonplandii*, *Parapiptadenia rigida* and *Cupania vernalis* occurred frequently in the ridgetop transect. On the one hand 13 species did not present a topographic association due to wide distribution through the gradient. By the other hand, the distinction between environmental and spatial effects showed that space contributes significantly on the distribution of tree species (Fig. 3). Environmental variables selected by forward selection procedure ($P < 0.05$) are summarized in Table 5. All geographical terms of the polynomial function were significant ($P < 0.05$) during spatial CCA and were add to the model. The four CCA analyses give the following results:

1. CCA of the species matrix constrained by the environmental matrix: sum of all canonical eigenvalues = 0.944; Monte Carlo tests for overall analysis: $F = 2.86$, $P < 0.001$;
2. CCA of species matrix constrained by spatial matrix: sum of all canonical eigenvalues = 1.017; Monte Carlo tests for overall analysis: $F = 3.59$, $P < 0.001$;
3. Environmental partial CCA (after removing the effect of geographical matrix): sum of all canonical eigenvalues = 0.416; Monte Carlo tests for overall analysis: $F = 1.35$, $P < 0.001$;

4. Spatial CCA (after removing the effects of environmental matrix): sum of all canonical eigenvalues = 0.489; Monte Carlo tests for overall analysis: F = 1.78, P < 0.001.

The total variation in the species matrix (total inertia) was 4.238. According to Borcard *et al*. (1992), the percentage of the total variation in the species matrix accounted for different steps (partition) is numbered as follows: (a) non-spatial environmental variation (0.416 × 100/4.238 = 9.81%; (b) spatially-structured environmental variation [(0.944 – 0.416) × 100/4.238 or (1.017 – 0.489) × 100/4.238 = 12.46%]; (c) non-environmental spatial variation (0.489 × 100/4.238 = 11.53%) and (d) unexplained non-spatial variation (100 – 33.8 = 66.2%).

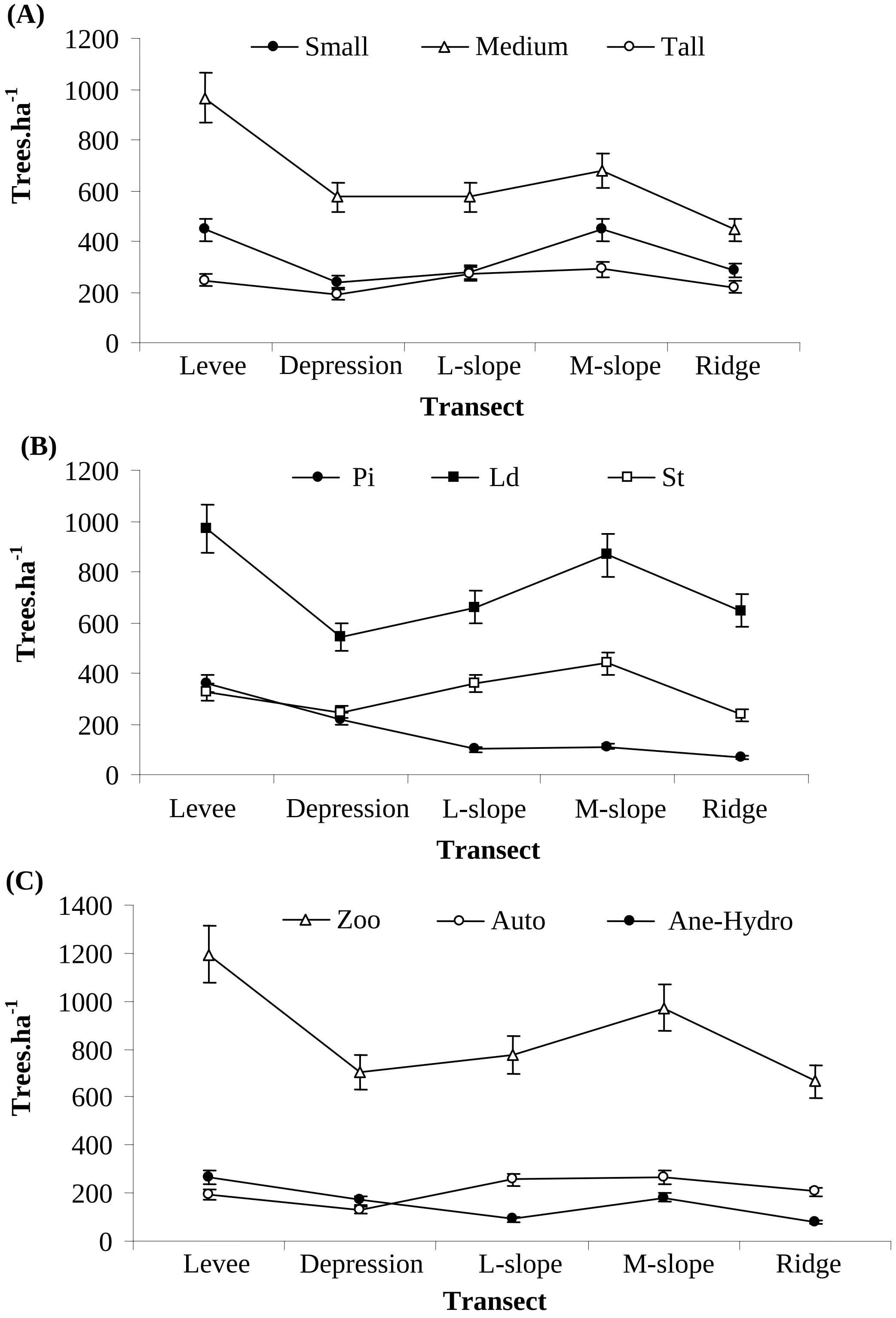


Figure 2. Trees per ecological groups of regeneration (A), vertical distribution (B) and dispersal (C) in five transects of riverine forest of Rio Botucaraí, Southern Brazil. Pi = Pioneer, Ld =

Light-demanding, St = Shade-tolerant; Zoo = Zoochorous, Auto = Autochorous, Ane = Anemochorous, Hydro = Hydrochorous.

Biplots of environmental variables and species or environmental variables and sampling units were depicted with the environmental partial analyses results (Fig. 4). In this step, species distributions are purely based on species-environment relationships. The first two axes accounted respectively for 26.8% (eigenvalue = 0.112) and 18.1% (eigenvalue = 0.075) of the species-environment relationships and species-environment correlations for these axes were 0.742 and 0.649 ($P < 0.05$) respectively. The first four axes accounted for 69.1% of species-environment relationships. Table 5 shows the intraset correlations among variables and canonical coefficients with the first two axes. The first canonical axis was positively correlated with topography and several soil variables that are influenced by flooding events. Percentages of organic matter, saturation of bases and cation exchange capacity where higher through upper sites, whereas aluminium contents were higher in lower areas. Thus, this environmental gradient may affect tree distribution patterns by restricting or facilitating species establishment. As related in the Indicator Analysis (although not accounting for spatial patterns directly), typical species of flooding areas occurred near the levee and depression and the zonation was sharp once frequent species of well-drained areas occurred only in the middle slope and ridgetop. Sampling units (Fig. 5) also appeared distributed according to the toposequence with some overlapping due to species distribution.

Rarefaction curves of species revealed significant differences on the expected total number of species in each transect with higher richness within the middle slope (Fig. 6 A). A regression model (Fig. 6 B) fitted diversity in a second-order polynomial regression ($y = -0.0586x^2 + 0.3594x + 2.91$, $R^2 = 0.77$) that showed the same pattern of species richness.

Table 5. Intraset correlations among environmental variables selected for the model during “environmental” partial CCA of the species matrix and canonical coefficients of the first two axes. Environmental variables were selected by forward stepwise selection and included on the model if significant in Monte Carlo tests ($P < 0.05$).

	Topography	Sand	P	K	Al	OM	V	CEC	Flooding
Topography									
Sand	-0.02								
P	-0.08	0.254							
K	0.588	-0.003	0.453						
Al	-0.336	0.368	-0.023	-0.552					
OM	0.625	0.046	0.226	0.706	-0.615				
V	0.304	0.035	0.323	0.680	-0.754	0.769			
CEC	0.252	0.159	0.001	0.322	-0.315	0.579	0.574		
Flooding	-0.804	-0.042	0.253	-0.218	0.040	-0.422	0.059	-0.203	
Axis 1	0.700	0.156	-0.08	0.537	-0.592	0.814	0.605	0.632	-0.678
Axis 2	0.132	-0.186	-0.365	-0.240	0.361	-0.185	-0.618	0.158	-0.445

Discussion

Environmental and spatial patterns

Tree species distribution throughout the topographical gradient indicated that both environmental and spatial features were particularly important in predicting species and community patterns. This agree with the well-knowing influence of geomorphic features and hydrological regimes on riparian forests over different temporal and spatial scales (Tabacchi et al. 1998, Turner et al. 2004, Désilets & Houle 2005), although distinctions between environmental and spatial effects remain poorly studied (Titeux et al. 2004). Here, we employed a routine to partialling out the spatial effects on the analysis of species-environment relationships that also highlight the spatial component embedded in such analysis (Legendre 1993). Once several biotic processes as growth, mortality, dispersal and predation influence the observed distributions of organisms (resulting in spatial correlation) or their distributions are dependent from explanatory variables which are themselves spatially-structured (Legendre 1993, Titeux et al. 2004), spatial structuring is an intrinsic component of ecosystems. In our analysis, ‘pure’ spatial trends were more attributed on the species distribution than ‘pure’ environmental effects, which link contagious biological processes as also important to the tree species distribution. By other hand, species and environmental data have a reasonable proportion of similar spatial structuring, identified by the largest proportion on the species variation due to spatially structured environmental variation (12.46%). According to Borcard et al. (1992) species and environmental variables have, in this case, the same response to some common underlying causes, as the topographic-flooding gradient. In fact, several studies have demonstrated the direct effect of wetting and desiccation processes on both mineralogy and the microbial ecology of the sediment, including nutrient dynamics (Baldwin & Mitchell 2000).

Once sediment or soils are submerged, the inundation leads to a decrease in oxygen contents and then resulting in progressive anaerobic conditions. Rapid cycling of litter may occur due to an increase on microbial activity that generates pulses on nutrient contents and then resulting in highly productive systems (Baldwin & Mitchell 2000). On the other hand, a negative effect is the rapid oxygen consumption leading quickly to the soil hypoxia or anoxia. After flood ending, the anaerobic zones of the sediments are newly oxygenated and microbiota is replaced gradually to a new phase.

Other spatially-structured variables are sediment deposition and litter displacement, which are not covered in our study. As demonstrated in ‘várzea’ forests of Amazonia (Witmann et al. 2004), sediment deposition decrease toward upper sites and species colonizing such lower areas frequently present specific adaptations to the new site conditions, regarding to adventitious roots that probably offer mechanical support (Parolin et al. 2004, Witmann et al. 2004). On the other hand, litter removal or deposition, including seed bank may affect directly species distribution once flooding and allied effects reallocating litter and seeds among sites (Johansson et al. 1996). Moreover, studies have showed that flooding timing, frequency and magnitude can be used as an indicator of sapling zonation on floodplain forests (Vreugdenhil et al. in press).

All these processes are included in the unmeasured variables or spatially-structuring processes that have been missed by the geographical terms (Titeux et al. 2004) and accounted to the far unexplained variation (66.2%). As also stressed by these authors, the stochastic space-time fluctuations of each population, the ‘unsaturation’ pattern (some species do not use all suitable habitats) and species recording in not appropriated spatial scales also contribute to this unexplained variation. Notwithstanding, occurrence data or species abundances are often noisy (ter Braack 1995) and not uncommon in ecological studies (Borcard & Legendre 1994, Titeux et al 2004).

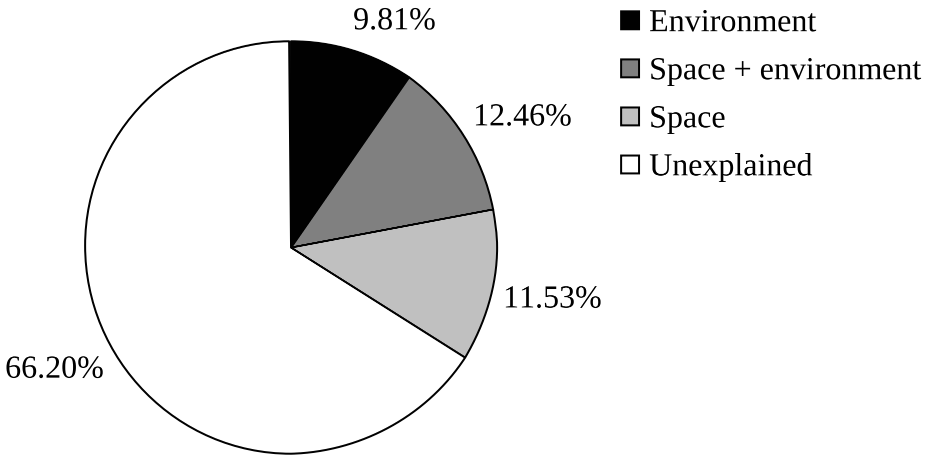


Figure 3. Variation partitioning of the tree species matrix.

Richness and diversity patterns

Significant transitions occurred from the levee and depression to the following lower slope transect, regarding to stand structure and ecological groups. Inversions on the proportion of pioneer/shade-tolerant trees and auto-hydrochorous to anemochorous trees occurred in that slightly transition and affected not only ecological groups but also species occurrences. As a consequence, this zonation transect may consist spatially as a boundary for tolerant and intolerant trees with regard to flooding. In fact, few species occurred over the entire flooding gradient and the lower slope also appears as an edge for several species.

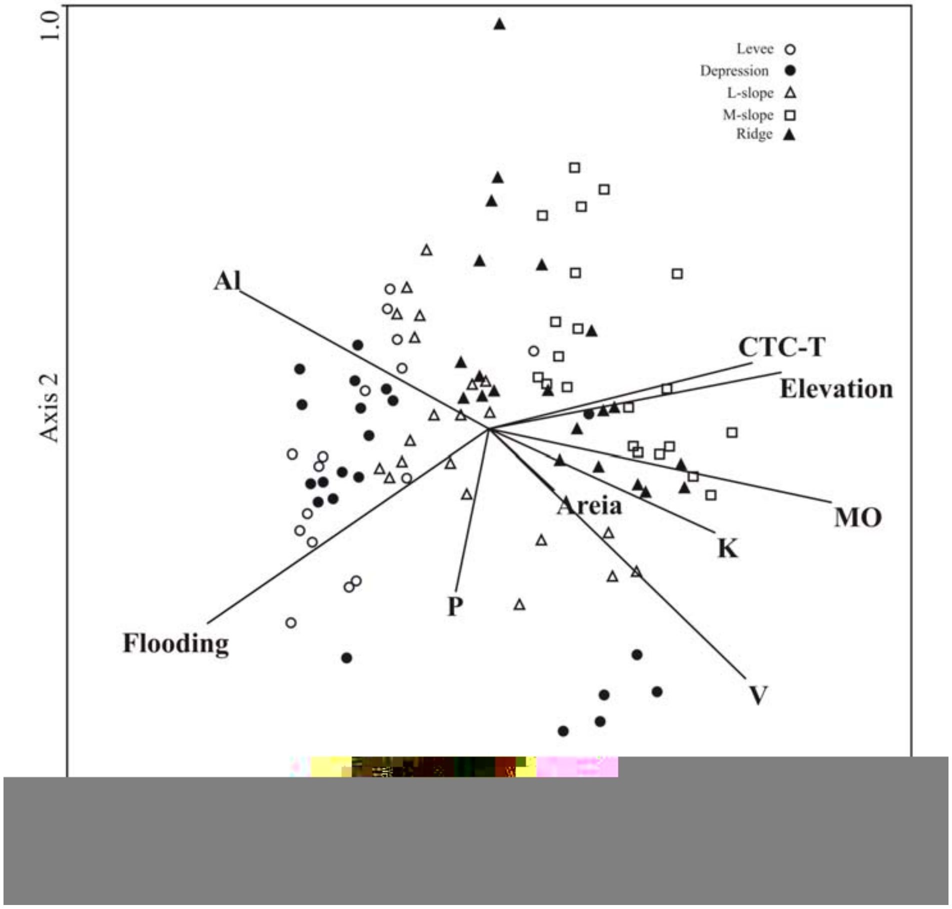


Figure 4. Ordination biplot depicting the two axes of the environmental partial CCA of sampling units in a riverine forest in Southern Brazil. Each sampling unit was identified by different symbols according to the respective transect. Environmental variables are represented their acronyms (see Table 2).

In a temporal scale, this area will probably present more heterogeneous spans in flooding events and then, it may consist in the most heterogeneous temporal-spatial sector across the topographic gradient, as related by Pollock et al. (1998) from different wetlands with different flooding regimes. In that view, structured over the dynamic-equilibrium model (Huston 1994), different patches from different seral stages are resulted from spatial variation of disturbance frequencies. If disturbance frequencies vary over time, a landscape could also contain patches of different seral stages (Pollock et al. 1998). These authors used that assumption in a model with temporally synchronous disturbance and found that at the community-scale level, the results supported many predictions of the dynamic-equilibrium model, especially regarded to species richness.

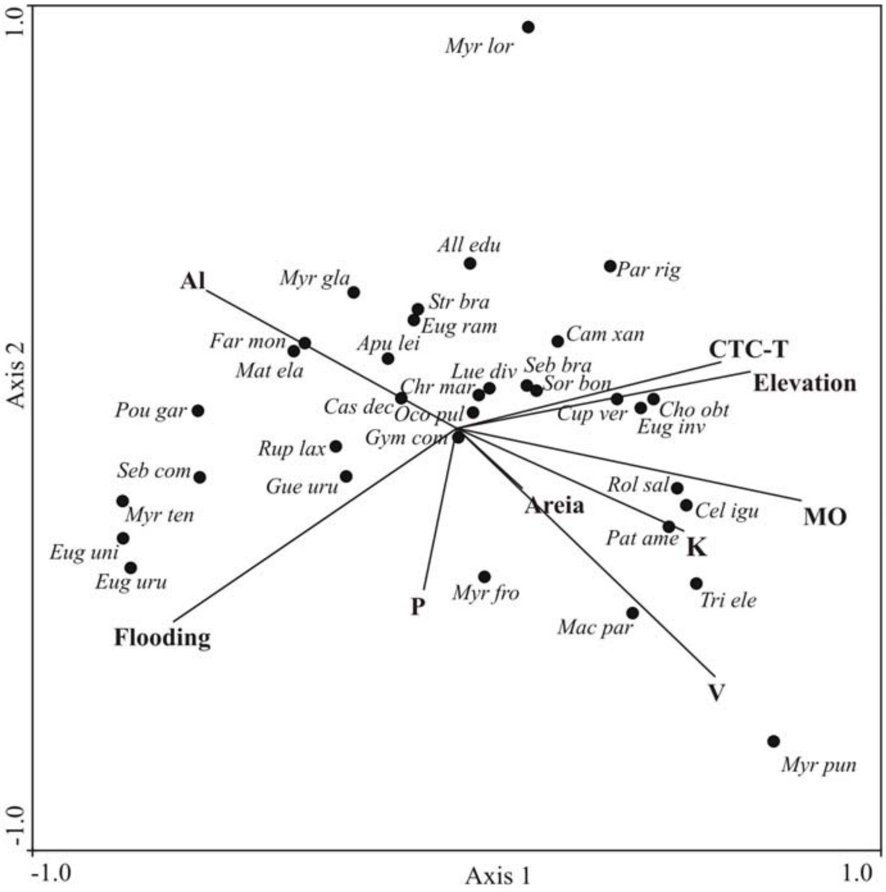


Figure 5. Ordination biplot depicting the two axes of the environmental partial CCA of species of a riverine forest in Southern Brazil. Species and environmental variables are represented by their acronyms (see table 2).

In our study, there are two major factors related to disturbance frequency. First and foremost is that once river floods are unpredictable, due to a hydrological regime that varies with occasional long-rainy periods, temporal heterogeneity should be higher than in areas with seasonal predicted floods; and second, microtopography must create spatial heterogeneity during floods events. On the other hand, well-drained upper sites are probably more affected by inherent community processes as gap-phase dynamics and direct supply rates of light (Stevens & Carson 2002). As related by Worbes et al. (1992) and Parolin (2001) hundreds of tree species with different phenological and ecological traits grow in seasonal flooded forests. In such cases, the cyclic alternation on floods and droughts drove species to life history, behavioral and morphological adaptations (Lytle & Poff 2004) but, in the case of unpredictable floods and droughts, as assigned in our study, bet-hedging strategies might be evolved, for example, by persistent seed bank or assynchronous reproductive phenologies (Brock et al. 2003), although there are no conclusive studies related to this theory (Lytle & Poff 2004).

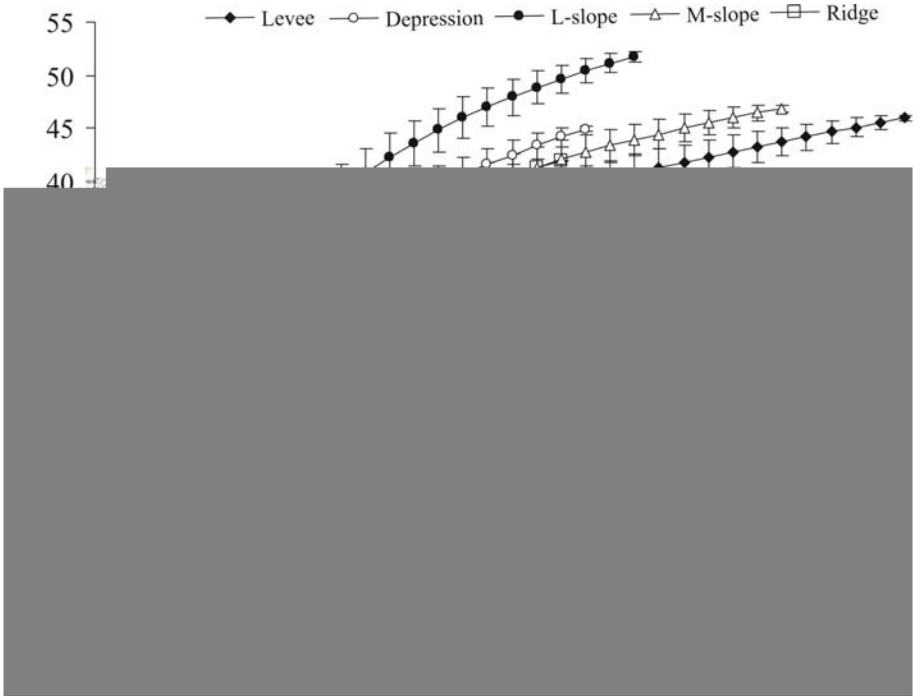


Figure 6. Rarefaction curves of tree species and Shannon diversity indices from five transects of riverine forest on the Rio Botucaraí, Southern Brazil Sampling units are representing different transects.

Allowed by a transition in the ecological groups from the lower sites to the upper ones, species richness has a maximum at the lower slope transect probably due to higher heterogeneity in disturbance events (space and time) and correlated variables. As reported by Désilets & Houle (2005), the spatial gradient provides some evidence for stress tolerance and competition as factors structuring species distribution across the topographic-flooding gradient, also boosted by an unpredictable pattern of floods that vary in frequency, timing and magnitude. Lower sectors showed predicted ecological groups already described for these areas (Budke et al. 2007, Junk et al. 1989, Lytle & Poff 2004) and expected structuring changes also occurred toward upper sites where the proportion of shade-tolerant and small trees increased, as well as anemochorous trees.

In summary, spatial-temporal and environmental variables are arranging tree species distribution across the toposequence of our study site. Furthermore, predicted ecological groups reflected the dynamics of disturbance in the topographic-hydrological gradient. Species richness and diversity also reflected such gradient and were higher in the mid-sector, where occasional floods should prevent competitive exclusion and generate high environmental heterogeneity.

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References

Baldwin, D.S., Mitchell, A.M. 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. Regul. Rivers: Res. Manage. 16, 457–467.

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.

Borcard, D., Legendre, P., Drapeau, P. 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

ter Braak C.J.F. 1995. Ordination. In: Jongman R.H.G., ter Braak C.J.F., van Togeren O.F.R (eds.). Data analysis in community and landscape ecology. Cambridge University Press, New York. pp. 91–173.

ter Braack, C.J.F., Smilauer, P. 1998. Canoco reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4.0). Microcomputer Power: Ithaca.

Brock, M.A. 2003. Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. Freshwater Biology 48, 1207–1218.

Budke, J.C., Athayde, E.A. Giehl, E.L.H., Záchia, R.A., Eisinger, S.M. 2005. Composição florística e estratégias de dispersão de espécies lenhosas em uma floresta ribeirinha, arroio Passo das Tropas, Santa Maria, RS, Brasil. Iheringia Bot. 60, 17–24.

Budke, J.C., Jarenkow, J.A., Oliveira-Filho, A.T. 2007. Relationships between tree component structure, topography and soils of a riverine forest, Rio Botucaraí, Southern Brazil. Plant Ecol. 189: 187–200.

Budke, J.C., Jarenkow, J.A., Oliveira-Filho, A.T. in press. Tree community features of two stands of riverine forest with different flooding regimes in Southern Brazil. Flora.

Cardoso, E., Schiavini, I. 2002. Relação entre distribuição de espécies arbóreas e topografia em um gradiente florestal na Estação Ecológica do Panga (Uberlândia, MG). Rev. Brasil. Bot. 25, 277–289.

Damasceno-Junior, G.A., Semir, J., Santos, F.A.M., Leitão-Filho, H.F. 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200, 119–135.

Désilets, P., Houle, G. 2005. Effects of resource availability and heterogeneity on the slope of the species-area curve along a floodplain-upland gradient. Journal of Vegetation Science 16, 487–496.

Dufrêne, M., Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345–366.

EMBRAPA. 1997. Manual de métodos de análises de solo. Empresa Brasileira de Pesquisa Agropecuária and Centro Nacional de Pesquisas de Solos, Rio de Janeiro.

Ferreira, C., Piedade, M.T.F., Parolin, P., Barbosa, K.M. 2005. Tolerância de *Himatanthus sucuuba* Wood. (Apocynaceae) ao alagamento na Amazônia Central. Acta Botanica Brasilica 19, 425–429.

Ferreira, L.V., Stohlgren, T.J. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. Oecologia 120, 582–587.

Ferreira, L.V. 2000. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. Biodiversity and Conservation 9, 1–14.

Gotelli, N.J., Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Lett. 4, 379–391.

Guilherme, F.A.G., Oliveira-Filho, A.T., Appolinário, V., Bearzoti, E. 2004. Effects of flooding regime and woody bamboos on tree community dynamics in a section of tropical semideciduous forest in south-eastern Brazil. Plant Ecol. 174, 19–36.

Huston, M. 1994. Biological diversity: the coexistence of species in changing landscapes. Cambridge University Press, Cambridge.

IPAGRO 1982. Atlas agroclimático do Rio Grande do Sul. Pallotti, Porto Alegre.

Johansson, M.E., Nilsson C., Nilsson, E. 1996. Do rivers function as corridors for plant dispersal? J. Veg. Sci. 7, 593–598.

Junk, W.J., Bayley, P.B., Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. Can. Publ. Fisher. Aquat. Sci. 106, 110–127.

Legendre. P. 1993. Spatial autocorrelation – trouble or new paradigm? Ecology 74, 1659–1673.

Leinz, V. 1949. Contribuição à geologia dos derrames basálticos do Rio Grande do Sul. Bol. Fac. Filos. Cienc. Let. São Paulo 58, 1–55.

Lytle D.A., Poff N.L. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19, 94–100.

McCune, B., Mefford, M.J. 1997. PC–ORD. Multivariate analysis of ecological data, version 4.36. MjM Software Design, Glaneden Beach.

Mueller-Dombois, D., Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley, New York.

Neiff, J.J. 1990. Ideas para la interpretación ecológica del Paraná. Interciencia 15, 424–441.

Oliveira-Filho, A.T., Vilela, E.A., Gavilanes, M.L., Carvalho, D.A. 1994. Effect of flooding regime and understory bamboos on the physiognomy and tree species composition of a tropical semideciduous forest in south-eastern Brazil. Vegetatio 113, 99–124.

Oliveira-Filho, A.T., Curi, N., Vilela, E.A., Carvalho, D.A. 2001. Variation in tree community composition and structure with changes in soil properties within a fragment of semideciduous forest in south-eastern Brazil. Edinb. J. Bot. 58, 139–158.

Parolin, P. 2001. Morphological and physiological adjustments to waterlogging and drought in seedlings of Amazonian floodplain trees. Oecologia 128, 326–335.

Parolin, P., de Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Piedade, M.T.F. & Junk, W.J. 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. The Botanical Review 70, 357–380.

Pijl, L.van der. 1982. Principles of dispersal in higher plants. Springer, New York.

Pillar, V.D. 2006. MULTIV. Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling, version 2.3.20. Departamento de Ecologia UFRGS, Porto Alegre.

Pollock, M.M., Naiman, R.J., Hanley, T.A. 1998. Plant species richness in riparian wetlands – a test of biodiversity theory. Ecology 79, 94–105.

Rosales, J., Petts, G., Knab-Vispo, C. 2001. Ecological gradients within the riparian forests of the lower Caura River, Venezuela. Plant Ecology 152, 101–118.

Stevens, M.H.H., Carson, W.P. 2002. Resource quantity, not resource heterogeneity, maintains plant diversity. Ecology Letters 5, 420–426.

Streck, E.V., Kämpf, N., Dalmolin, R.S.D., Klamt, E., Nascimento, P.C., Schneider, P. 2002. Solos do Rio Grande do Sul. EMATER/RS and UFRGS, Porto Alegre.

Swaine, M.D., Whitmore, T.C. 1988. On the definition of ecological species groups in tropical rain forests. Vegetatio 75, 81–86.

Tabacchi E., Correll D.L., Hauer R., Pinay G., Planty-Tabacchi A.M., Wissmar R. 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biology 40, 497–516.

Titeux, N., Dufrêne, M., Jacob, J. P., Paquay, M., Defourny, P. 2004. Multivariate analysis of fine-scale breeding bird atlas using a geographical information system and partial canonical correspondence analysis: environmental and spatial effects. Journal of Biogeography 31, 1841–1856.

Turner, M.G., Gergel, S.E., Dixon, M.D. & Miller, J.R. 2004. Distribution and abundance of trees in floodplain forests of the Wisconsin River: environmental influences at different scales. Journal of Vegetation Science 15, 729–738.

Vreugdenhil, S.J., Kramer, K. & Pelsma, T. 2006. Effects of flooding duration, frequency and depth on the presence of saplings of six woody species in north-west Europe. Forest Ecology and Manage. in press.

Walker, K.F., Sheldon, F., Puckridge, J.T. 1995. A perspective on dryland river ecosystems. Regul. Rivers: Res. Manage. 11, 85–104.

Weiher, E. 2003. Species richness along multiple gradients: testing a general multivariate model in oak savannas. Oikos 101, 311–316.

Wittmann, F., Junk, W.J., Piedade, M.T.F. 2004. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. For. Ecol. Manage. 196, 199–212.

Worbes, M., Klinge, H., Revilla, J.D., Martius, C. 1992. On the dynamics, floristic subdivision and geographical distribution of Várzea forests in Central Amazonia. J. Veg. Sci. 3, 553–564.

Zar, J.H. 1996. Biostatistical analysis. Prentice-Hall, New Jersey.

Capítulo IV

Tree species richness and flood pulses: a multivariate approach along a disturbance gradient in a riverine forest of Southern Brazil [5]

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Abstract

Several hypotheses have been developed to describe causes and patterns of plant species richness over space and time. We evaluated variation of tree richness in a forest gradient from a non-flooded forest to a riverside frequently flooded forest in Southern Brazil. We distributed four 1.0 ha plots across the topographical range and divided each plot in ten contiguous 100 m × 10 m transects where all individual trees with perimeter at breast height (pbh) $\geq$ 15 cm were sampled. A detailed topographical and soil survey was carried out across plots and indicated clearly differences in soil chemistry, organic and texture patterns. We evaluated a hypothesized model using structural equation modelling – SEM to observe relationships among environmental variables, disturbance and biomass in predicting tree species richness. The 5,779 surveyed trees belonged to 96 species and 37 families. Disturbance frequency indicated lower biomass toward lowland areas and it also played sharp influence over soil variables. The interaction between disturbance and biomass revealed a tree species richness peak at increased biomass and decreased disturbance frequency ($R^2 = 0.32$). The final structural accepted model explained 79% of tree species richness and 67% of variation on biomass. Transects' ordination revealed floristic and changes throughout the entire topographical gradient suggesting that habitat selection influences species distribution patterns. Overall, richness appears to be controlled by a set of direct and indirect effects, where disturbance frequency patterns played a specific role, followed by biomass and less by soil properties.

key words: Biomass, Flooding regime, Riverine forest, Soil properties, Structural equation modelling.

Introduction

Several hypotheses have been developed concerning different factors that affect or control plant species richness. Major specific factors include productivity and competition, disturbance and the species pool capable to establish in a site (Laughlin & Grace 2006). The complexity and magnitude of this issue reflected in a review (Grace 1999, see also Palmer 1994) where these authors counted more than a hundred theories describing causes and patterns of plant species and diversity. Generally, univariate models of productivity or disturbance were described as unimodal predictors of plant species richness and according to Cardinale et al. (2006) they had some success in explaining such patterns. On the other hand, environmental variables are frequently associated with the presence or absence of some species, according to its capacity to establish at a site or, the environmental influences on plant biomass (Gough et al. 1994). In the first case, environmental variables and disturbance may be associated given that disturbance can affect the availability or heterogeneity of specific variables in a system. This approach of disturbance defines it as the processes leading to either the survivors of disturbance or new colonists to respond to increased resources availability, then, accelerated growth of small individuals released from competition is a response pattern to disturbance (Glenn-Levin and van der Maarel 1992). The direct influence of disturbance on biomass led us to a second approach where distribution limits plant biomass by causing its partial or total destruction (Grime 1979) or as a change in conditions which interferes in the current functioning of a given biological system (Glenn-Levin & van der Maarel 1992).

The conceptual model of Dynamic Equilibrium (Huston 1994) proposed diversity is the result of community biomass production which leads to competitive exclusion and, disturbance, which may reduces, by itself, species density. Kondoh (2001) improved this model showing that relationships between species richness to productivity and disturbance are both unimodal, though the level of one factor that maximizes species richness depends on the level of the second factor, in a interaction not previously accounted by univariate causal models (Cardinale et al. 2006).

In the past few years, multivariate hypotheses development and testing methods have conducted to increasing efforts in evaluate hypotheses concerning networks of controlling factors on species richness, specially the structural equation modelling (Grace & Pugesek 1997, Weiher 2003, Laughlin & Grace 2006). This approach depends on the use of theoretically-specified models of plausible relationships and to test and determine which models are consistent or not with the multivariate relations in the data (Grace 2006). Consistent models can indicate the role different factors play in a system and the strengths of different pathways (Laughlin & Grace 2006). According to these models, several factors presented evidence to regulate plant species richness, most of them addressed to herbaceous plant communities (Grace & Pugesek 1997, Grace 1999, Weiher 2003, Weiher et al. 2004).

Flooding is recognized as playing great role in structuring plant communities in riverine forests. Different studies have demonstrated the consequences of prolonged water logging on both anatomical and physiological plant traits (Koslowski 2002, Lytle & Poff 2004) or the direct effects of floods on seed dynamics (Boedltje et al. 2004), population dynamics (Guilherme et al. 2004) or community structure (Wittmann et al. 2004, Budke et al. 2007, Oliveira-Filho et al. 2001). Neiff (1990) decomposed flooding as a function of frequency, intensity, tension, recurrence, amplitude and seasonality – *f* FITRAS (Neiff 1990, Neiff 1997) and, this perspective recognizes the direct influence of inundation pulses over plant species distribution and abundance.

In different cases, tree species richness were higher when flooding presented low frequency or intensity values (Ferreira & Stohlgren 1999, Ferreira 2000, Wittmann et al. 2004, Damasceno-Junior et al. 2005, Budke et al. 2007) agreeing with theory predicting that when flooding is periodic and of short duration, the associated nutrient inputs may contribute to increase diversity and productivity or, in the case of prolonged events, it represents a major stress and may reduce both species richness and productivity (Désilets & Houle 2005).

In this study we seek to evaluate a multivariate model of the relationships among environmental variables, disturbance and biomass in predicting tree species richness in riparian forests. Here, we argue that since flooding is a direct promoter of disturbance within riparian forests, then it is also the main resource of tree species variation across these systems. Our approach started by testing a general multivariate model linking environmental variables, disturbance and biomass in predicting tree species richness and providing an alternative model if necessary. Then, we decomposed disturbance (measured as flooding frequency per year) and biomass (measured in m^2. ha^{-1}) in a separated bivariate model to seek for specific contribution of these resources on tree species richness.

Methods

Study area

This research was conducted in the riparian fringes of Rio Botucaraí near its confluence with Rio Jacuí (30º01’S, 52º47’W) (Budke et al. 2007). The river headwaters lie in the southernmost extent of the high planes region locally knew as Planalto Meridional, made up of Cretaceous basalts originating from giant lava flows that covered the sedimentary lowlands of the Paraná basin (Leins 1949). Downstream, at its mid-course the Rio Botucaraí reaches sedimentary lowlands and the topography is dominated by recently flood-deposited sediments, meanders and point bars. At its lower course, near the study area, flooding events are enhanced by the confluence with the stronger adjoining stream flow of the Rio Jacuí, therefore promoting lateral overflow.

The regional climate is moist subtropical, without a regular dry season; the mean annual temperature and rainfall are 19.2 ºC and 1,594 mm.year^{-1}, respectively (IPAGRO, 1982). The predominant soil is a Hydromorphic Planosol, with typical stratified layers of depositional sediments (Streck et al., 2002). Floods in the area are highly unpredictable because there is no one marked seasonal rainy period and rainfall is relatively well distributed throughout the year. As a consequence, floods occur at any time of the year. The duration of overflow periods may vary from some days to a few weeks.

Sampling design

We distributed four 1 ha (100 × 100 m) plots in a toposequence from the river margin of the Rio Botucaraí to a non-flooded forest site. Each plot comprised ten contiguous 100 × 10 m transects parallel to the river margin. Forest structure and relationships of each discrete plot were described in earlier papers (Budke et al. 2006, Budke et al. 2007, Lindenmaier & Budke 2006, Budke et al. in press). All individual living trees, having at least one stem with perimeter at breast height (pbh) $\geq$ 15 cm were sampled. Voucher material of different species was collected, prepared and lodged in the Herbarium ICN of the Universidade Federal do Rio Grande do Sul.

We carried out a detailed topographic survey of the transects using a 10 m long water-filled levelling hose, 3/8 in., a tape measurer and a compass, according to Cardoso and Schiavini (2002). The resulting grid of vertical positions was used to produce contour maps and to obtain the relative elevation to the river, which was used to interpolate with flooding pulses.

We collected samples of the topsoil (0-20 cm depth) from 60 sites distributed in different positions, in such a way that its overall topographic variation was encompassed. The soil samples were kept in polyethylene bags and taken to the UFRGS Soil Laboratory for chemical and textural analyses. The measured variables were: cation exchange capacity (CEC – $cmol_c/dm^3$), which is defined as an excellent fertility estimator and comprises potassium (K), calcium (Ca), magnesium (Mg) and sodium (Na) cations (hereafter named *fertility*); pH in water; aluminium saturation (Al-%), organic matter (OM-%) and soil texture (hereafter named *texture*), which encompasses clay, silt and sand proportions. All procedures followed EMBRAPA (1997) protocol.

As a disturbance promoting variable, flooding is commonly associated as a major factor on structure and dynamics of riparian forests (see introduction). Here, we used an attribute of flooding (flooding frequency) to express relations with tree species richness. Flooding frequency is defined as the number of times floods have occurred in a time period (years, decades, centuries) (Neiff 1996), then it is an intrinsic measurable component of the flood pulse (Neiff 1996). To estimate flooding frequency in each transect we crossed the relative elevation of each transect and the hydrometer records of Rio Jacuí station (data calibrated according to topography). Through Pulse 1.1.1 software (Neiff & Neiff 2003) we estimated the mean number of floods per year from 1981 to 2004 and we used this variable as a disturbance estimate in each transect (hereafter named *disturbance*).

The hypothesized model

Based both on previous multivariate investigations of plant species richness by structural equation modelling (Grace & Pugesek 1997, Weiher et al. 2004, Désilets & Houle 2005, Laughlin & Grace 2006) and several works relating different environmental variables describing tree species structure and dynamics in riparian forests (Oliveira-Filho et al. 1994, van den Berg & Oliveira-Filho 1999, Ferreira & Stohlgren 1999, Damasceno-Junior et al. 2005, Rosales et al.

2001) we developed an initial model based on hypothesized relationships among variables and tree species richness (Fig. 1). In the model, all variables were directly related to tree species richness and, as we expected, some of the predictors to be indirectly related to richness, by a set of correlated causes (flooding frequency affecting *fertility* mean values, by example) then, we related different endogenous variables to be caused by flooding frequency (also endogenous) or slope (Fig. 1).

In order to produce a general hypothesized model, we initially included an exogenous variable called *elevation*, which is not assumed to be caused by any variable described in the model. After *elevation*, we included flooding frequency as a specifically measure of *disturbance* and we related three latent soil variables, far recognized as influencing tree species distribution and abundance (Oliveira-Filho et al. 1994, van den Berg & Oliveira-Filho 1999, Rosales et al. 2001). First, a *chemistry* variable was included and the initial assumption was that it would be correlated with pH, Al and fertility (measured variables). Second, we included an *organic* latent variable, measured by organic matter (%) and third, a *texture* variable was included, which was measured by clay, sand and silt proportions. These variables seek to determine if tree species richness relates in some way to disturbance and the roles of some environmental variables (majority soil variables) in predicting species richness. As recognized by Laughlin & Grace (2006) is not easy to guarantee all the processes operating in the system will be represented by causal relations implied by these assumptions. Therefore, the aim is to determine whether data relationships are consistent with expectation from any of the hypotheses generated (Bollen 1989, Laughlin & Grace 2006). After set plausible explanatory variables we included biomass in the model due to its direct and indirect potential effects in controlling species richness (reviewed by Huston 1994, Grace 1999). In this case, we did not account for density effects on richness which is commonly associated to diversity indices, though we also had interest in evaluating whether density affected richness. Then, we regressed richness related to density per transect and we observed density did not account in predict tree species richness ($r^2 = 0.002$, $P = 0.6$). The final hypothesized model (Fig. 1) included both the relationships among latent variables (structural model) and the relationships between latent and indicator variables (measurement model) (Grace & Pugesek 1997).

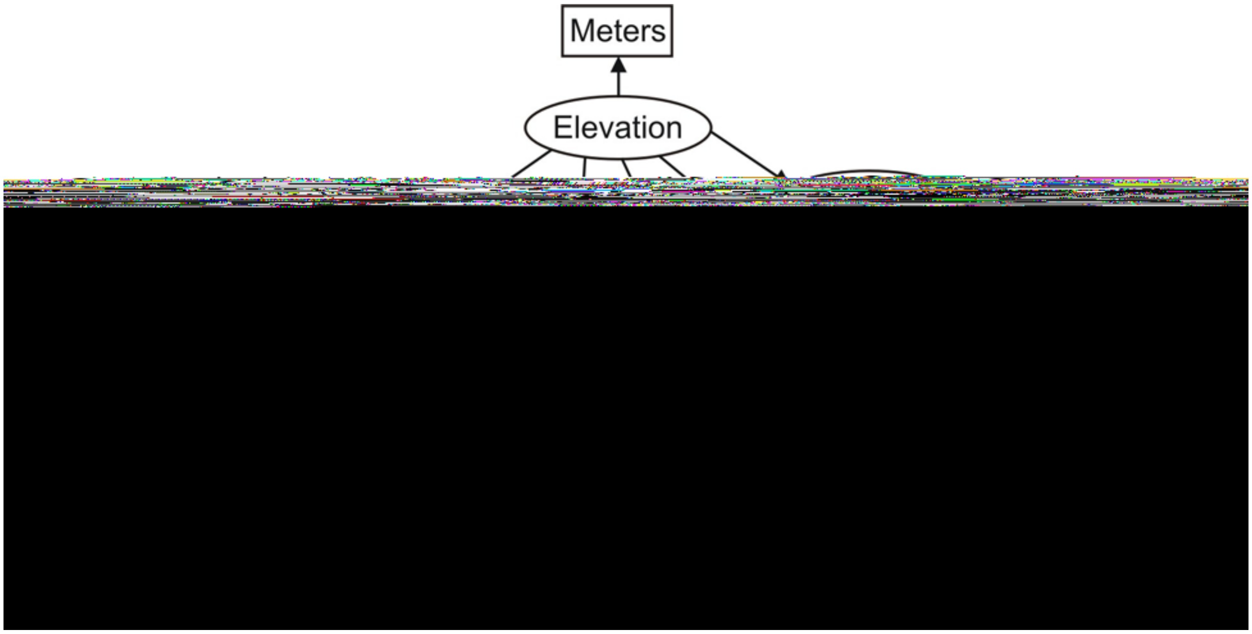


Figure 1. Initial (hypothetical) structural model showing the relationships among latent variables (ellipses) of the subtropical riverine forest of Rio Botucaraí, Southern Brazil. Measured variables and respective units were indicated in boxes.

Data analysis

We used Principal Coordinates Analysis (PCoA) to obtain orthogonal axes describing the community resemblance among transects with Jaccard's coefficient as the similarity measure. In order to achieve for linearity among relationships and establish a common scale among variables to perform the structural equation modelling, transformations were performed when needed. We generally followed the steps outlined by Laughlin & Grace (2006) and Weiher et al. (2004). The software used to perform the analyses was AMOS 4 (Arbuckle & Wothke 1999). Prior the evaluation of the full model, we examine bivariate relations among variables, all of which in the 40 transects (0.1 ha). The protocol used to evaluate alternative models was described by Pugesek & Garce (1997) where several alternative models are compared with the initial model to test the best fit and parsimony. Finally, the best model is identified and estimated. We used the minimum fit function χ^2 to verify how the data fitted the models. Alternatively, we used the root mean square error of approximation – RMSEA and the goodness of fit index – GFI which tests for an acceptable fit between a model and data (Désilets & Houle 2005).

To evaluate whether species richness will be a function of disturbance frequency and biomass as an increasing function of their interactions (Kondoh 2001), we evaluated this prediction testing richness to a second-order polynomial function, as performed by Cardinale et al. (2006), according to the equation:

$$S = b_0 + b_1B + b_2D + b_3B^2 + b_4D^2 + b_5B \times D + \varepsilon$$

where D is the disturbance frequency (mean no. floods year^{-1}) and B is an estimative of biomass [estimated by basal area (m^2.ha^{-1})].

Results

The studied area has well-defined geomorphic features that include point bars with recent-deposited sediments, meanders and small ponds located in the lower sites, which reflect river dynamics and associated sedimentation. Across the entire topographical range, we observed that soil texture corresponded to such variations (Fig. 2). Frequently flooded transects presented high proportion of silt, or sand in some cases. Sand proportion was higher at upper non-flooded sites, although, some upper transects also presented low sand proportion. Clay, by other hand presented low proportion among all transects and varied only from 10 to 30 percent. Silt proportion was higher at low to moderate elevated sites but it also varied lesser than sand proportions (Fig. 2).

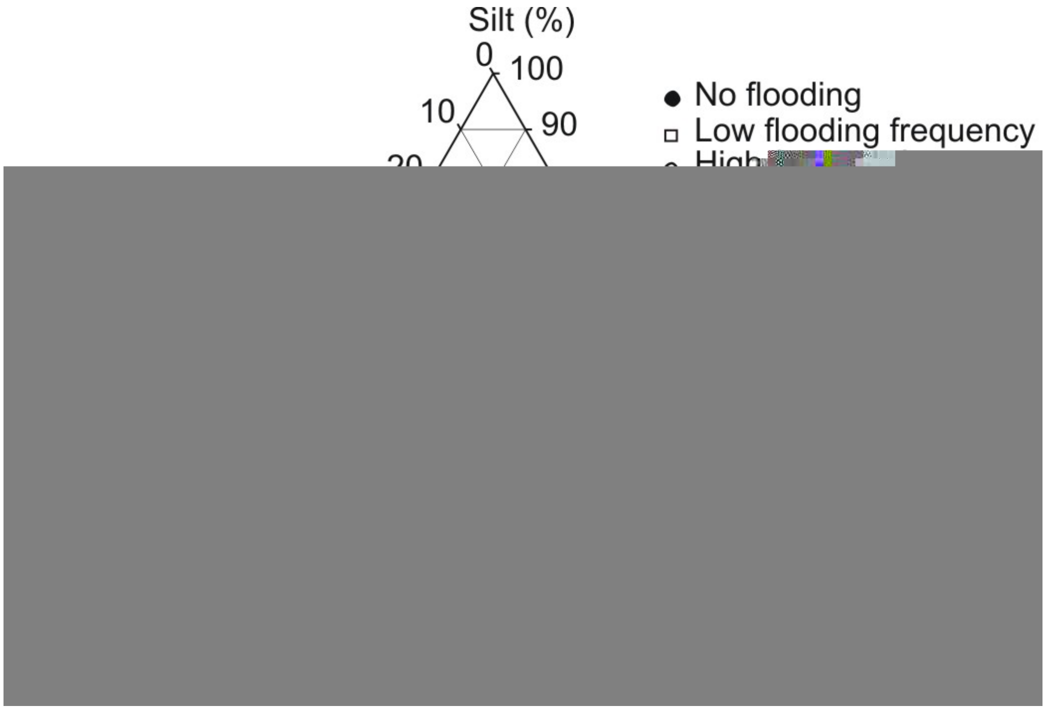


Fig. 2. Proportions of sand, silt and clay from different transects located in forest remnants under different flooding regimes of rio Botucaraí, Southern Brazil.

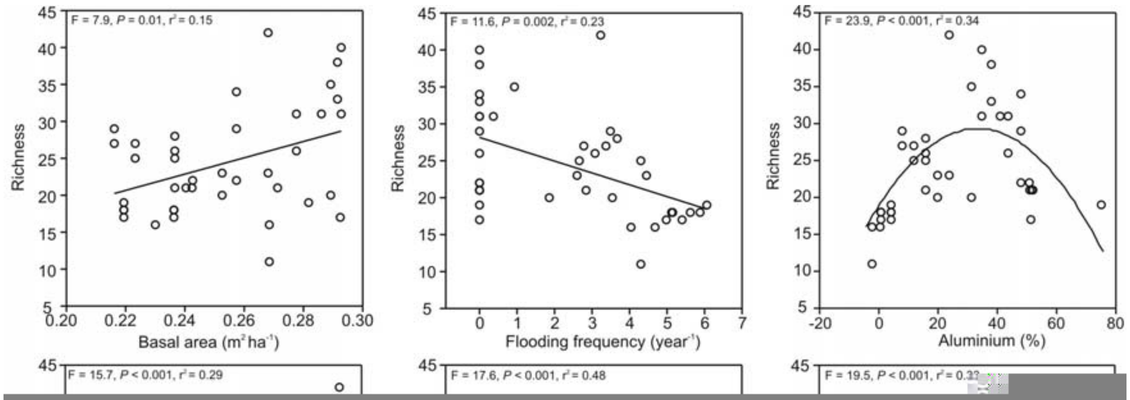
Field inventory yielded a total of 5,779 trees belonging to 96 species and 36 families, from which, Myrtaceae (14) and Fabaceae (13) were the richest families, followed by Euphorbiaceae, Rubiaceae, Salicaceae and Sapotaceae, each with five tree species (see Apêndices). The first two axes of the PCoA ordination explained *ca*. 30% of the total variation (Axis 1 = 21.9%; Axis 2 = 8%) and the transects arrangement indicated there is a strong species gradient, starting at the left side, with non-flooded forest transects and ends at the right side, with frequently flooded forest transects (Fig. 3).

Fig. 3. Ordination plot showing floristic similarities among transects located in forest remnants under different flooding regimes in Southern Brazil, yielded by PCoA.

All predictor variables included in the analysis presented strong relationships with tree species richness (Fig. 4), which had its maximum at intermediate elevation. Peak richness occurred at high fertility soils, high organic matter and intermediate levels of aluminium saturation. Only seven transects presented high proportion of aluminium (saturation > 50%) and most transects had intermediate-low fertility (saturation < 50%) which means soils presented low to moderated fertility but without major aluminium restrictions to nutrient absorption by plants. Richness declined severely with the increase of disturbance and it reached a peak at low disturbance frequency. By other hand, highest richness appeared at intermediate to high biomass levels (Fig. 4). Disturbance also affected aluminium saturation, while fertility remained unaffected (Fig. 4). Disturbance fit a linear relationship with biomass fairly well ($r^2 = 0.45$), with decreasing biomass toward higher disturbance. Aluminium and fertility also fitted biomass well both with positive lines, which were expected since these variables also decreased toward higher disturbance. Correlations among all latent variables indicated different degrees of relation among them (Table 1).

After analyzing for the adequacy of our initial model, with major interest on the relationships among latent variables, a preliminary fit indicated some measured variables did not figure as consistent variables in the model and did not contribute in explaining any additional information when considered as isolated latent variables, thus, they were deleted from the final model. These variables were: proportions of silt and clay, aluminium saturation and pH. Furthermore, some pathways were also deleted from the model, including those from soil chemistry and soil texture on biomass and soil texture on richness. Three pathways were included in the final model and represented direct interactions of soil texture and soil chemistry on soil organic and soil texture on soil chemistry.

Final analysis of the revised full model indicated that the model obtained a close fit with the data ($\chi^2_{df=3} = 1.724$, $P = 0.63$; RMSEA = 0.000, $P = 0.667$; GFI = 0.988), where GFI values higher than 0.9 indicate good fit between model and data. Testing for other relationships in this model revealed none other meaningful pathways either due to increased instability or absence of significance, then, we accepted this model as the best of all other previously considered (Fig. 5).



[redacted]

Fig. 4. Linear and curvilinear regressions of tree species richness and biomass, soil properties (chemistry, organic and texture), aluminium saturation (transformed), fertility (expressed as Cation Exchange Capacity) in forest remnants under different flooding regimes in Southern Brazil.

Table 1. Pearson correlations among latent variables included in the structural equation modelling. Soil properties were assigned as chemistry, organic or texture variables.

	Elevation	Disturbance	Biomass	Chemistry	Organic	Texture	Richness
Elevation	1						
Disturbance	-0.89***	1					
Biomass	0.52***	-0.67***	1				
Chemistry	0.17 ns	-0.21 ns	-0.49***	1			
Organic	0.74***	-0.75***	0.75***	0.69***	1		
Texture	0.44**	-0.24 ns	-0.23 ns	-0.53***	-0.17 ns	1	
Richness	0.22 ns	-0.48***	0.39**	0.54***	0.58***	-0.37*	1

*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns non-significant

The final model explained 79% of variation in richness and 67% of variation on biomass (Fig. 5) Disturbance was clearly associated to elevation, as a direct function of topography. Soil chemistry (expressed in the final model only by fertility), organic and texture (expressed by sand proportion only) were also well explained in the final model and, additional paths among them helped to explain organic matter contents and soil chemistry. Together, disturbance and elevation explained well the variation on soil texture ($r^2 = 0.34$). All variables helped to explain variation on tree species richness by direct or indirect effects (Table 2). Disturbance and elevation presented the highest direct effects on richness, followed by soil organic and less by biomass and soil chemistry. Disturbance also account for the highest direct effect on biomass, by a negative path, while soil organic account to biomass positively (Table 2).

Table 2. Standardized total, direct and indirect effects of predictor latent variables on species richness and tree biomass. Blanks indicate where relationships were not included in the model.

	Total effect	Direct effect	Indirect Effect
Effects on species richness			
Elevation	0.12	-0.87	0.92
Disturbance	-0.78	-0.88	0.08
Biomass	-0.33	-0.33	–
Soil chemistry	0.18	0.08	0.09
Soil organic	0.26	0.5	-0.22
Soil texture	-0.24	–	-0.24
Effects on biomass			
Elevation	0.28	-0.34	0.63
Disturbance	-0.57	-0.39	-0.17
Soil organic	0.37	0.37	–

The interaction between disturbance and biomass on tree species richness (Fig. 6) revealed a concave-down function with an increasing function of their interaction. Contrary to our expectation and previous models, richness reached a peak at increased biomass and at decreased disturbance frequency. The quadratic term explained 32.5% of variation on tree species richness (F = 4.2, $P < 0.001$).

Fig. 5. Final structural equation model for tree species richness from a riverine forest in Southern Brazil.

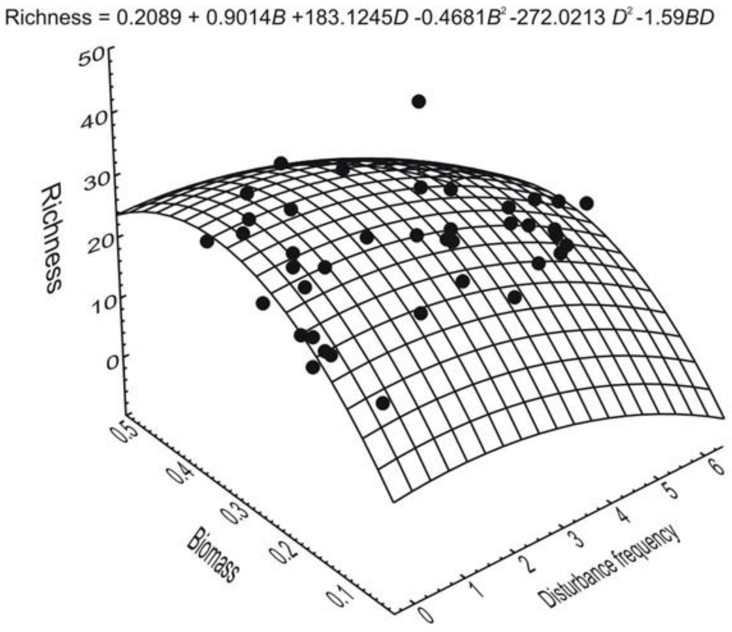


Fig. 6. Tree species richness as a function of disturbance frequency (mean no. floods.year^{-1}) and biomass (m^2.ha^{-1}) fitted with a quadratic polynomial function (see methods).

Discussion

Spatial patterns of environmental variables

It is well know that flood pulses influence several environmental variables by changing either its availability or heterogeneity (Neiff 1997, Pollock et al. 1998, Baldwin & Mitchell 2000, Houle & Desiléts 2005). In topography gradients, as related in our study, these variations are more evident because elevation promotes spatial patchiness at local or regional scale, which are correlated with soil properties and hydrological conditions (Myamoto et al. 2003, Budke et al. 2006, Budke et al. in press). According to Araújo & Haridasan (1988) catenary soils frequently present increasing aluminium saturation toward upper sites, where soil lixiviation already removed most of cation contents and aluminium remain unaltered (Chen et al. 1997). Soil texture also reflects the geomorphic scenery of a specific area and flooding regime because both sediment deposition and removal are promoted by flood events. Across the entire studied area, clay contents were low, although some microsites presented high clay contents due to slow water movement (Budke et al. 2007). Schiavini (1997) detailed these lower sites near river margin and recognized different geomorphic sectors: dike, depression and slope or edge. According to this author and other works (Oliveira-Filho et al. 1994, Ward et al. 2002, Wittmann et al. 2004) flooding is assigned as the major factor in structuring soil layers in these areas, where frequently stratified layers of litter, sediment and other material occur (Budke et al. 2007). Sand and silt followed the same pattern and can be described as derived from geomorphic features and hydrological regime. Whereas sand fraction was higher at upper sites, silt contents increased toward lower ones, but differences in silt contents remain low among transects, and it resulted in silt and clay subtraction on the final model. By other hand, fertility presented a more complex distribution pattern. Different works have demonstrated fertility being higher close to the river margins, where soil dynamics increase environmental heterogeneity (Schiavini 1997, Oliveira-Filho et al. 2001). However, flooding duration or frequency may produce a negative effect on soil fertility by increase acidification or decrease nutrient contents (Rezende et al. 2002). Across the studied area fertility was higher at low disturbance frequency and several transects were considered as distrophic ones. To tree species, the interaction between aluminium and fertility play a specific role on distribution patterns. In riparian forests of the lower Caura River, biogeochemical gradients were primary drivers of tree species distribution, together with hydraulic disturbance (Rosales et al. 2001).

Flooding, as a direct measure of disturbance, presented different frequencies across the topographical range and it was a causal variable to most of the other environmental parameters. As described above, flooding acts directly on tree species by seed bank removal and deposition (Boedeltje et al. 2004), plant damage and waterlogging or indirectly, by decrease soil oxygen (Joly 1996) and interacting with other variables as soil texture and fertility (Oliveira-Filho et al. 1994, Budke et al. 2006a).

In the Botucaraí basin, like other low-order rivers (Budke et al. 2006), flooding is not a long-lasting event. In the Amazonian basin, for example, the period of inundation can last up to 270 days (Ferreira & Stholgren 1999). By other hand, flooding frequency in the studied basin is high and some point bars or depressions can be subject of several inundations yearly, leading to small ponds where tree richness is fairly low (Budke et al. 2006a, 2007a). Budke et al. (2007a) detailed forest structure of lower sites of the Rio Botucaraí and they recognized not only an early successional stage in those areas but also monoespecific patches of flooding-tolerant trees as *Sebastiania commersoniana* and *Eugenia uruguayensis*. Flooding acts in this basin by unpredictable events and it plays a substantial role in structuring tree species, not only by seed bank removal or sediment dynamics but also by it high variable flow regime. In this case, flexible and opportunistic live history strategies are more likely to develop (Walker et al. 1995).

Patterns of tree species richness

Mechanisms driving variation in riparian forests are hard to summarize because the complex suite of interacting factors operating at multiple spatial and temporal scales (Baker & Wiley 2004). Researches have frequently reported different results in describing tree species richness and structure (Robertson 2006, Ferreira 2000, Damasceno-Junior et al. 2005, Turner et al. 2004). In the riparian forest of Rio Botucaraí, disturbance was particularly important in predict tree richness both by direct and indirect effects and, as expected, it was far relevant to explain the variation on biomass and environmental variables. Together, disturbance and biomass clearly reflected the variation on tree richness but, should they reflect variation on tree composition?

In point bar forests of south-eastern USA coastal plain, streamside vegetation receives short and frequent non-predictive floods, which cause significant mortality of trees or seedlings of most species (Robertson 2006). In such forests, mortality occurs mainly in the initial recruitment stages, then, selective environment seems to be more predictive on tree composition than competition. Between the two lower plots (Budke et al. 2007b) biomass did not changed, although it had high variables at micro-scale (0.01 ha), due to patches in the forest structure. On this hand, our findings support disturbance to predict species richness rather than biomass but, this trend is scale-dependent. Furthermore, ecological groups (Budke et al. 2006a, Budke et al. 2007b) provided substantial sources to predict lower biomass toward higher disturbance by both small trees predominance and absence of emergent-tall trees. This figure agrees with the quadratic relation of disturbance and biomass on the variation of tree richness. In moderate-high disturbance frequency sites, again, pioneer trees create dense patches and, although this functional group may present higher primary production (Grime 1979), habitat selection keeps these areas as poor-species sites.

Other models gave the same assumptions, as pointed out by Cardinale et al. (2006). According to these authors when frequency disturbance is low and biomass production still high, selection is expected to favour dominance of competitively superior species because: there is sufficient time for recruitment; there is time for local interactions come to influence community structure and because inferior competitors may be extinct from the system. By other hand, the authors conclude when disturbance frequently is still high and biomass production low, conditions benefit both dispersal-adapted species to exploit spatial gaps unoccupied by superior competitors and those adapted to resist disturbance or recover quickly.

Modelling tree richness to causal variables

Structural equation modelling (SEM) has only been recently explored by biological issues and the number of applications is steadily increasing (Grace & Pugesek 1997, Scheiner et al. 2000, Iriondo et al. 2003, Grace 2006). Generalized from multiple regression, SEM allows one to estimate the strength and sign of directional relationships on models with several causal variables and dependent relations, over *a priori* hypothesized scheme. Different from multiple regression, SEM analyses relations in subsequent periods, whereas the former operates simultaneously on fitting data and model with no *a priori* structured hypotheses.

The final model explained high proportion of the variation on tree richness (R^2 = 0.79), although we did not account to other underlying processes as gap analysis, edge effects or other landforms. In riparian forests of Wisconsin River, landscape configuration only influenced species presence and abundance in recent developed forests (Turner et al. 2004) with geographic province performing better than soils in predict species composition. In our study, aluminium saturation and soil fertility were lesser predictors than disturbance on tree richness prediction, though, the indirect effects of soil properties should aggregate considerable explanation. Notwithstanding, the soil texture gradient showed presumably covariation on richness due to its dependence from disturbance events and geomorphic features (elevation, declivity). Thus, the indirect effects of elevation are greater than the direct effects, substantially because it influences inundation and soil variables.

Budke et al. (third chapter) described forest structure of the plot located at infrequent flooded sites and the authors pointed out species distribution and abundance were spatial autocorrelated and this trend do not be discarded on describing ecological phenomena (Legendre 1993). Although we not directly account to spatial autocorrelation, it is presumably that underlying effects as soil properties and species occurrence covary in the space, thus accounting to the high richness variance explained. Another point is that our findings are scale-dependent, designed in a 0.1 ha scale. In broad-scale as regional or geographical metrics (also long-time scale) other processes including climatic fluctuation and plant species migration play a predominant role, mainly on the species pool of riparian landscapes (Renöfält et al. 2005). On a functional perspective, anatomical and physiological traits able plant species resist to several limitations, which allows colonizing and designing different patches, not covered in this study.

It is noteworthy that tree richness patterns were consistent to some previous theoretical models, natural surveys and experiments (Huston 1994, Oliveira-Filho et al. 1994, Pollock et al. 1998, Turner et al. 2004, Houle & Desiléts 2005, Cardinale et al. 2006), but with some peculiar differences as the inverse relation between disturbance and biomass on predict tree richness. Here, however, there is a limitation that is we have considered basal area as a direct measure of productivity. Although it would have been better to measure primary production on each transect, it is far impractical, then, basal area provides a direct useful measure of cumulative biomass, which, according to Cardinale et al. (2006), would be otherwise complicated to get.

A perspective for riparian forests conservation

Several works have demonstrated the influence of flood pulses in structuring plant communities in riverscapes, wetlands and other environments around the world (Neiff 1997, Pollock et al. 1998, Hughes et al. 2003, Parolin et al. 2004, Wittmann et al. 2004) and the consequences of changing water regimes over different communities (Andersson et al. 2000, Nilsson & Svedmark 2002, Kozlowski 2002, Hughes 2003, Lytle & Poff 2004). Although river flow regimes have been regulated in the past few decades, our capability to understand such effects on natural systems remains incomplete.

Univariate explanations frequently fail in predictind diversity, due mostly to its limited power over a wide range of variables underlying such patterns. Structural equation modelling and other multivariate approaches predict synergistic effects of variables on species diversity (Cardinale et al. 2006) that became better approaches in predict human impacts over water courses. Our study suggests that disturbance is the major factor in structuring tree communities in rivers where flooding events are unpredictable. When structured with biomass and other environmental variables, they far explained richness patterns across the studied area. This conclusion has implications on the management of riparian ecosystems in Southern Brazil, where several rivers remain endangered by large dam projects or dredging. Moreover, studies underlined to predict functional types through these areas are needed to understand how habitat selection acts on life history, behaviour and morphological traits in riparian landscapes.

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References

Andersson, E., Nilsson. C. & Johansson, M.E. 2000. Effects of river fragmentation on plant dispersal and riparian flora. Regulated Rivers: Research and Management 16: 83–89.

Araújo, G.M. & Haridasan, M. 1988. A comparison of the nutritional status of two forest communities on mesotrophic and dystrophic soils in Central Brazil. Soil Science and Plant Analysis 19: 1075–1089.

Arbuckle, J.L. & Wothle, W. 1999. Amos 4.0 user's guide. SmallWaters Corporation, Chicago.

Baldwin, D.S. & Mitchell, A.M. 2000. The effects of drying and re-flooding on the sediment and soil nutrient dynamics of lowland river-floodplain systems: a synthesis. Regulated Rivers Research and Management 16: 457–467.

Baker, M.E. & Wiley, M.J. 2004. Characterization of woody species distribution in riparian forests of lower Michigan, USA using map-based models. Wetlands 24: 550–561.

Boedeltje, G., Bakker, J., ten Brinke, A., van Groenendael, J.M. & Soesbergen, M. 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. Journal of Ecology 92: 786–796.

Bollen, K.A. 1989. Structural equation with latent variables. John Wiley & Sons, London.

Budke, J.C., Jarenkow, J.A., Oliveira-Filho, A.T. & Lindenmaier, D.S. 2006. Padrões de riqueza e diversidade em rios de pequeno porte. In: Mariath, J.E.A. & Santos, R.P. (eds.). *Os avanços da botânica no início do século XXI*. SBB, Porto Alegre.

Budke, J.C., Jarenkow, J.A., Oliveira-Filho, A.T. 2007. Relationships between tree component structure, topography and soils of a riverine forest, Rio Botucaraí, Southern Brazil. Plant Ecology 189: 189–200.

Budke, J.C., Jarenkow, J.A. & Oliveira-Filho, A.T. in press. Tree community features of two stands of riverine forest under different flooding regimes in Southern Brazil. Flora.

Budke, J.C., Jarenkow, J.A. & Oliveira-Filho, A.T. Distribution of tree species and relationships with spatial and environmental variables in a riverine forest of Southern Brazil. (Third Thesis Chapter).

Cardinale, B.J., Hillebrand, H. & Charles, D.F. 2006. Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. Journal of Ecology 94: 609–618.

Chen, Z., Hsieh, C., Jiang, F., Hsieh, H. & Sun, I. 1997. Relations of soil properties to topography and vegetation in a subtropical rain forest in southern Taiwan. Plant Ecology 132: 229–241.

Cardoso, E., Schiavini, I. 2002. Relação entre distribuição de espécies arbóreas e topografia em um gradiente florestal na Estação Ecológica do Panga (Uberlândia, MG). Rev. Brasil. Bot. 25, 277–289.

Damasceno-Junior, G.A., Semir, J., Santos, F.A.M. & Leitão-Filho, H.F. 2005. Structure, distribution of species and inundation in a riparian forest of Rio Paraguai, Pantanal, Brazil. Flora 200: 119–135.

Désilets, P. & Houle, G. 2005. Effects of resource availability and heterogeneity on the slope of the species-area curve along a floodplain-upland gradient. Journal of Vegetation Science 16: 487–496.

EMBRAPA. 1997. Manual de métodos de análises de solo. Empresa Brasileira de Pesquisa Agropecuária and Centro Nacional de Pesquisas de Solos, Rio de Janeiro.

Ferreira, L.V. 2000. Effects of flooding duration on species richness, floristic composition and forest structure in river margin habitat in Amazonian blackwater floodplain forests: implications for future design of protected areas. Biodiversity and Conservation 9: 1–14.

Ferreira, L.V. & Stohlgren, T.J. 1999. Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. Oecologia 120: 582–587.

Glenn-Levin, D.C. & van der Maarel, E. 1992. Patterns and process of vegetation dynamics. In: Glenn-Levin, D.C., Peet, R.K. & Veblen, T.T. (eds.). *Plant sucession, theory and prediction*. Chapman & Hall, London.

Gough, L., Grace, J.B., Taylor, K.L. 1994. The relationship between species richness and community biomass: the importance of environmental variables. Oikos 70: 271–279.

Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. Perspectives in Plant Ecology, Evolution and Systematics 2: 1–28.

Grace, J.B. 2006. Structural equation modeling and the study of natural systems. Cambridge University Press, Cambridge.

Grace, J.B. & Pugesek, B.H. 1997. A structural equation model of plant species richness and its application to a coastal wetland. The American Naturalist 149: 436–460.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley & Sons, London.

Guilherme, F.A.G., Oliveira-Filho, A.T., Appolinário, V. & Bearzoti, E. 2004. Effects of flooding regime and woody bamboos on tree community dynamics in a section of tropical semideciduous forest in south-eastern Brazil. Plant Ecology 174: 19–36.

Hughes, F., Richards, K., Girel, J., Moss, T., Muller, E., Nilsson, C. & Rood, S. 2003. The flooded forest: guidance for policy makers and river managers in Europe on the restoration of floodplain forests. University of Cambridge, Cambridge.

Huston, M. 1994. Biological diversity: the coexistence of species in changing landscapes. Cambridge University Press, Cambridge.

IPAGRO 1982. Atlas agroclimático do Rio Grande do Sul. Pallotti, Porto Alegre.

Iriondo, J.M., Albert, M.J. & Escudero, A. 2003. Structural equation modelling: and alternative for assessing causal relationships in threatened plant populations. Biological Conservation 113: 367–377.

Joly, C.A. 1996. The role of oxygen diffusion to the root system on the flooding tolerance of tropical trees. Revista Brasileira de Biologia 56: 375–382.

Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. Proceedings of the Royal Society of London Series B 268: 269–271.

Koslowski, T.T. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. Wetlands 22: 550–561.

Laughlin, D.C. & Grace, J.B. 2006. A multivariate model of plant species richness in forests systems: old-growth montane forests with a long history of fire. Oikos 114: 60–70.

Legendre. P. 1993. Spatial autocorrelation – trouble or new paradigm? Ecology 74, 1659–1673.

Leinz, V. 1949. Contribuição à geologia dos derrames basálticos do Rio Grande do Sul. Boletim da Faculdade de Filosofia, Ciências e Letras da USP 58, 1–55.

Lindenmaier, D.S. & Budke, J.C. 2006. Florística, diversidade e distribuição espacial das espécies arbóreas de uma floresta estacional na bacia do rio Jacuí, sul do Brasil. Pesquisas Botânica 57: 193–216.

Lytle D.A. & Poff N.L. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19: 94–100.

Myamoto, K., Suzuki, E., Kohyama, T., Seino, T., Mirmanto, E. & Simbolon, H. 2003. Habitat differentiation among tree species with small-scale variation of humus depth and topography in a tropical health forest of Central Kalimantan, Indonesia. Journal of Tropical Ecology 19: 43–54.

Neiff, J.J. 1990. Aspects of primary productivity in the lower Paraná and Paraguay riverine system. Acta Limnologica Brasiliensia 3: 77–113.

Neiff. J.J. 1996. Large rivers of South America: toward the new approach. Verhandlungen Internationale Vereinigung Limnologie 26: 167–180.

Neiff, J.J. 1997. El régimen de pulsos en ríos y grandes humedales de Sudamérica. In: Malvarez, A.I. & Kandus, P. (eds.). Tópicos sobre grandes humedales sudamericanos. ORCYT-MAB/UNESCO, Montevideo.

Neiff, J.J. & Neiff. M. 2003. Pulso: software para análisis de fenómenos recurrentes. URL: www.neiff.com.

Nilsson, C. & Svedmark, M. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. Environmental Management 30: 468–480.

Oliveira-Filho, A.T., Curi, N., Vilela, E.A. & Carvalho, D.A. 2001. Variation in tree community composition and structure with changes in soil properties within a fragment of semideciduous forest in south-eastern Brazil. Edinburgh Journal of Botany 58: 139–158.

Oliveira-Filho, A.T., Vilela, E.A., Gavilanes, M.L. & Carvalho, D.A. 1994. Effect of flooding regime and understory bamboos on the physiognomy and tree species composition of a tropical semideciduous forest in south-eastern Brazil. Vegetatio 113: 99–124.

Palmer, M. 1994. Variation in species richness: towards a unification of hypotheses. Folia Geobotanica & Phytotaxonomica 29: 511–530.

Parolin, P., de Simone, O., Haase, K., Waldhoff, D., Rottenberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schmidt, W., Piedade, M.T.F. & Junk, W.J. 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. The Botanical Review 70: 357–380.

Pollock, M.M., Naiman, R.J. & Hanley, T.A. 1998. Plant species richness in riparian wetlands – a test of biodiversity theory. Ecology 79: 94–105.

Renöfält, B.M., Nilsson, C. & Jansson, R. 2005. Spatial and temporal patterns of species richness in a riparian landscape. Journal of Biogeography 32: 2025–2037.

Robertson, K.M. 2006. Distributions of tree species along point bars of 10 rivers in the south-eastern US Coastal Plain. Journal of Biogeography 33: 121–132.

Rosales, J., Petts, G. & Knab-Vispo, C. 2001. Ecological gradients within the riparian forests of the lower Caura River, Venezuela. Plant Ecology 152: 101–118.

Schiavini I. 1997. Environmental characterization and groups of species in gallery forests, In: Proceedings of the International Symposium on Assessment and Monitoring of Forests in Tropical Dry Regions with Special Reference to Gallery Forests. UNB, Brasília.

Scheiner, S.M., Mitchell, R.J. & Callahan, H.S. 2000. Using path analysis to measure natural selection. Journal of Evolutionary Biology 13: 423–433.

Streck, E.V., Kämpf, N., Dalmolin, R.S.D., Klamt, E., Nascimento, P.C. & Schneider, P. 2002. Solos do Rio Grande do Sul. EMATER/RS and UFRGS, Porto Alegre.

Turner, M.G., Gergel, S.E., Dixon, M.D. & Miller, J.R. 2004. Distribution and abundance of trees in floodplain forests of the Wisconsin River: environmental influences at different scales. Journal of Vegetation Science 15: 729–738.

Van den Berg E. & Oliveira-Filho A.T. 1999. Spatial partitioning among tree species within an area of tropical montane gallery forest in south-eastern Brazil. Flora 194: 249–266.

van den Broek, T. van Diggelen, R. & Bobbink, R. 2005. Variation in seed buoyancy of species in wetland ecosystems with different flooding dynamics. Journal of Vegetation Science 16: 579–586.

Walker, K.F., Sheldon, F. & Puckridge, J.T. 1995. A perspective on dryland river ecosystems. Regulated Rivers: Research and Management 11: 85–104.

Ward, J.V., Tockner, K., Arscott, D.B. & Claret, C. 2002. Riverine landscape diversity. Freshwater Biology 47: 517–539.

Weiher, E. 2003. Species richness along multiple gradients: testing a general multivariate model in oak savanas. Oikos 101: 311–316.

Weiher, E., Forbes, S. & Shauwecker, T. & Grace, J.B. 2004. Multivariate control of plant species richness in a blackland prairie. Oikos 106: 151–157.

Wittmann, F., Junk, W.J. & Piedade, M.T.F. 2004. The várzea forests in Amazonia: flooding and the highly dynamic geomorphology interact with natural forest succession. Forest Ecology and Management 196: 199–212.

Conclusão final

Os padrões de distribuição de espécies arbóreas e grupos ecológicos ao longo da floresta ribeirinha do rio Botucaraí demonstraram que o regime de inundação possui grande importância sobre a estrutura da floresta e seleção sobre os grupos ecológicos predominantes em cada cota de elevação em relação ao rio. Da mesma forma, as variações nas propriedades físico-químicas do solo estão associadas à dinâmica hidrosedimentar, entretanto, possuem papel menor na variação de riqueza de espécies ao longo da área. Espécies características de estádios iniciais de sucessão são mais abundantes em áreas de menor elevação, formando muitas vezes, densos agrupamentos com poucas espécies. Por outro lado, a estrutura vertical torna-se mais complexa nos sítios mais elevados, com o aumento de árvores de sub-bosque e indivíduos emergentes. A análise em escala local revelou que existe elevada autocorrelação espacial na distribuição das variáveis ambientais e espécies arbóreas em determinada escala, tornando extremamente relevante a mensuração do efeito causado pelo espaço sobre padrões encontrados. A interação entre freqüência de distúrbio e biomassa explicou cerca de 32% na variação de riqueza de espécies, enquanto que a utilização de um modelo estrutural multivariado demonstrou ser mais eficiente ($R^2 = 0.79$) em explicar a variação na riqueza de espécies. A análise de espécies indicadoras revelou a existência de espécies com distribuição restrita a determinados sítios, sendo a freqüência de distúrbio, uma variável extremamente eficiente em predizer a ocorrência das espécies. Estas informações fornecem importante subsídio para estudos ligando fatores condicionantes sobre a estrutura e dinâmica de comunidades e populações de espécies arbóreas, bem como informações para a recuperação de florestas ribeirinhas e a necessidade de manutenção de pulsos de inundação para a manutenção da integridade destes ambientes.

Referências bibliográficas

Ab'Saber, A.N. 2000. O suporte geoecológico das florestas beiradeiras (ciliares). Pp. 15-26. In: Rodrigues, R.R. & Leitão-Filho, H.F. (eds.). Matas ciliares: conservação e recuperação. São Paulo: EDUSP/FAPESP.

Arbuckle, J.L. & Wothle, W. 1999. Amos 4.0 user's guide. SmallWaters Corporation, Chicago.

Benedito-Cecílio, E. & Agostinho, A.A. 2000. Distribution, abundance and use of different environments by dominant ichthyofauna in the influence area of Itaipu reservoir. Acta Scientiarum 2: 429-437.

Bigarella, J.J. 2003. Estrutura e origem das paisagens tropicais e subtropicais. Volume III. Florianópolis: UFSC.

ter Braack, C.J.F., Smilauer, P. 1998. Canoco reference manual and user's guide to Canoco for Windows: software for canonical community ordination (version 4.0). Microcomputer Power: Ithaca.

Cardoso, E. & Schiavini, I. 2002. Relação entre distribuição de espécies arbóreas e topografia em um gradiente florestal na Estação Ecológica do Panga (Uberlândia, MG). Revista Brasileira de Botânica 25, 277–289.

Cardinale, B.J., Hillebrand, H. & Charles, D.F. 2006. Geographic patterns of diversity in streams are predicted by a multivariate model of disturbance and productivity. Journal of Ecology 94: 609-618.

Cruz, R.C. 2005. Prescrição de vazão ecológica: aspectos conceituais e técnicos para bacias com carência de dados. Tese (Doutorado em Ecologia). Porto Alegre: Universidade Federal do Rio Grande do Sul, 176 f.

Dunn, R.R., Colwell, R.K. & Nilsson, C. 2006. The river domain: why are there more species halfway up the river? Ecography 29: 251–259.

Gotelli, N.J., Colwell, R.K. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Lett. 4, 379–391.

Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assesment. Perspectives in Plant Ecology, Evolution and Systematics 2: 1-28.

Huston, M. 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101.

Huston, M. 1994. Biological diversity: the coexistence of species in changing landscapes. Cambridge: Cambridge University Press.

Junk, W.J., Bayley, P.B. and Sparks, R.E. 1989. The flood pulse concept in river-floodplain systems. Can. Publ. Fisher. Aquat. Sci. 106, 110–127.

Kandus, P. & Adamoli, J.M. 1993. Freshwater marsh vegetation response to flooding patterns in the lower delta of the Parana river. Wetlands Ecology and Management 2: 213-222.

Kandus, P., Kalesnik, F., Borgo, L. & Malvárez, A.I. 2002. La reserva natural Isla Botija en el delta del rio Paraná: análisis de las comunidades de plantas y condicionantes ambientales. Parodiana 12: 3-20.

Kondoh, M. 2001. Unifying the relationships of species richness to productivity and disturbance. Proceedings of the Royal Society of London Series B 268: 269-271.

Koslowski, T.T. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. Wetlands 22, 550–561.

Lindenmaier, D.S. & Budke, J.C. 2006. Florística, diversidade e distribuição espacial das espécies arbóreas de uma floresta estacional na bacia do rio Jacuí, sul do Brasil. Pesquisas Botânica 57: 193–216.

Lytle, D.A. 2001. Disturbance regimes and life history evolution. American Naturalist 157: 525-536.

Lytle, D.A. & Poff, N.L.R. 2004. Adaptation to natural flow regimes. Trends in Ecology and Evolution 19(2): 94–100.

McCune B. and Mefford M.J. 1997. PC-ORD. Multivariate analysis of ecological data, version 3.0. MjM Software Design, Oregon Glaneden Beach.

Mereles, M.F. 2004. Los humedades en Paraguay: principales tipos de vegetación. Pp. 67-89. In: Salas-Duenãs, D., Mereles, M.F. & Yanosky, A. (eds.). Los humedales de Paraguay. RAMSAR, Fundación Moisés Bertoni, Comité Nacional de Humedales, Paraguay.

Mereles, M.F. 2005. Una aproximación al conocimiento de los sistemas de humedales de la futura Reserva de Biosfera del Chaco boreal, Paraguay. Pp. 70-77. In: Reyes, L.F. & Moura, D.M. (eds.). Humedales de Ideroamérica, experiencias de estudio e gestión. CYTED, Red Iberoamericana de Humedales: Asunción.

Molino, J.F. & Sabatier, D. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypotheses. Science 294: 1702-1704.

Mueller-Dombois, D., Ellenberg, H. 1974. Aims and methods of vegetation ecology. John Wiley, New York.

Neiff, J.J. 1990. Aspects of primary productivity in the lower Paraná and Paraguay riverine system. Acta Limnologica Brasiliensia 3: 77-113.

Neiff, J.J. 1997. El régimen de pulsos en ríos y grandes humedales de Sudamérica. Pp. 1-49. In: Malvarez, A.I. & Kandus, P. (eds.). Tópicos sobre grandes humedales sudamericanos. Buenos Aires: ORCYT-MAB/UNESCO.

Neiff, J.J., Iriondo, M.H. & Carignan, R. 1994. Large tropical south american wetlands: an overview. Pp. 156-165. In: Link, G.L. & Naiman, R.J. (eds). The Ecology and Management of Aquatic-terrestrial Ecotones. Washington: Washington University.

Nilsson, C., Svedmark, M. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. Environ. Manage. 30, 468–480.

Oliveira-Filho, A.T., Vilela, E.A., Gavilanes, M.L. & Carvalho, D.A. 1994. Effect of flooding regime and understory bamboos on the physiognomy and tree species composition of a tropical semideciduous forest in south-eastern Brazil. Vegetatio 113, 99–124.

Parolin, P., Armbruester, N., Wittmann, F., Ferreira, L.V., Piedade, M.T.F. & Junk, W.J. 2002. A review of tree phenology in central Amazonian floodplains. Pesquisas Botânica 52: 195-222.

Parolin, P., DeSimone, O., Haase, K., Waldhoff, D., Rottemberger, S., Kuhn, U., Kesselmeier, J., Kleiss, B., Schimidt, W., Piedade, M.T.F. & Junk, W.J. 2004. Central Amazonian floodplain forests: tree adaptations in a pulsing system. The Botanical Review 70: 357-380.

Pausas, J.G. & Austin, M.P. 2001. Patterns of plant species richness in relation to different environments: an appraisal. Journal of Vegetation Science 12: 153–166.

Petts, G.E. 1994. Rivers: Dynamic components of catchments ecosystems. Pp. 3–22. In: Calow, P. & Petts, G.E. (Eds.). The Rivers Handbook II. Oxford: Blackwell.

Pillar, V.D. 2006. MULTIV. Multivariate Exploratory Analysis, Randomization Testing and Bootstrap Resampling, version 2.3.20. Departamento de Ecologia UFRGS, Porto Alegre.

Pollock, M.M., Naiman, R.J., Hanley, T.A. 1998. Plant species richness in riparian wetlands – a test of biodiversity theory. Ecology 79, 94–105.

Poole, G. 2002. Fluvial landscape ecology: addressing uniqueness within the river discontinuum. Freshwater Biology 47: 641-660.

Ribeiro, J.F. & Walter, B.M.T. 1998. Fitofisionomias do bioma Cerrado. Pp. 47-86. In: Sano, S.M. & Almeida, S.P. (eds.) Cerrado: ambiente e flora. Planaltina: Embrapa.

Ribeiro, J.F. & Walter, B.M.T. 2001. As matas de galeria no contexto do bioma Cerrado. Pp. 29-47. *In*: J.F. Ribeiro, C.E.L. Fonseca & J.C. Sousa-Silva (eds.). Cerrado: caracterização e recuperação de matas de galeria. Planaltina, Embrapa Cerrados.

Rodrigues, R.R. 2000. Uma discussão nomenclatural das formações ciliares. Pp. 91-100. In: Rodrigues, R.R. & Leitão-Filho, H.F. (eds.) Matas ciliares: conservação e recuperação. São Paulo: EDUSP/FAPESP.

Schreiner O.H. 2003. Avaliação da disponibilidade de água na bacia do rio Botucaraí para atender à demanda do arroz irrigado. Dissertação (Mestrado em Engenharia Hidráulica). Canoas: Universidade Luterana do Brasil. 112 f.

Schwarzbold, A. 2000. O que é um rio? Ciência & Ambiente 21: 57–68.

Streck, E.V., Kämpf, N., Dalmolin, R.S.D., Klamt, E., Nascimento, P.C. & Schneider, P. 2002. Solos do Rio Grande do Sul. EMATER/RS and UFRGS, Porto Alegre.

Tabacchi, E., Correl, D.L., Hauer, R., Pinay, G., Planty-Tabacchi, A.M. & Wissmar, R.C. 1998. Development, maintenance and role of riparian vegetation in the river landscape. Freshwater Biology 40: 497–516.

Tedesco, M.J., Gianello, C., Bissani, C.A., Bohnem, H. & Volkweiss, S.J. 1997. Análise de solo, plantas e outros materiais. Porto Alegre, UFRGS.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton: Princeton University press.

Vannote, R.L, Minshall, G.W., Cummins, K.W., Sedell, J.R., Cushing, C.E. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130-137.

Vazzoler, A.E.A.M., Lizama, M.L.A.P. & Inada, P. 1997. Influências ambientais sobre a sazonalidade reprodutiva. Pp. 267-280. In: Vazzoler, A.E.A.M., Agostinho, A.A. & Hahn, N.S. (eds.). A planície de inundação do alto rio Paraná. Maringá: EDUEM.

Walker, K.F., Sheldon, F., Puckridge, J.T. 1995. A perspective on dryland river ecosystems. Regulated Rivers Research and Management 11, 85–104.

Ward, J.V., Tockner, K., Arscott, D.B. & Claret, C. 2002. Riverine landscape diversity. Freshwater Biology 47: 517–539.

Zar J.H. 1996. Biostatistical analysis. Prentice-Hall, New Jersey.

Apêndices

Apêndice 1.

Species density and ecological groups from the riverine forest of Rio Botucaraí, Southern Brazil., EG = ecological groups, P = pioneer, Ld = light-demanding and St = shade-tolerant; S = small, M = medium, T = tall; Zoo-Z = zoochorous, Ane = anemochorous, Aut = Autochorous.

Family/Species	**Density**	**EG**
Fabaceae		
Albizia edwalli (Hoehne) Barneby & Grimes	1	LD-E-Ane
Apuleia leiocarpa (Vogel) Macbr.	72	Ld-E-Ane
Parapiptadenia rigida (Benth.) Brenan	54	Ld-E-Aut
Myrocarpus frondosus Allem.	26	Ld-T-Ane
Mimosa bimucronata (DC.) Kuntze	1	P-M-Ane/Hid
Machaerium paraguariense Hassler	13	Ld-M-Ane
Enterolobium contortisiliquum (Veloso) Morong	9	Ld-E-Zoo
Dalbergia frutescens (Vell.) Britton	5	Ld-M-Ane
Lonchocarpus nitidus (Vogel) Benth.	5	Ld-M-Ane
Lonchocarpus campestris Mart ex Benth.	3	Ld-M-Ane
Inga vera Willd.	50	Ld-M-Zoo/Hyd
Erythrina falcata Benth.	1	Ld-T-Ane
Calliandra tweediei Benth.	3	Ld-M-Aut
Euphorbiaceae		
Gymnanthes concolor Spreng.	524	St-S-Aut
Sapium glandulosum (L.) Morong	4	P-S-Aut
Sebastiania schottiana (Müll. Arg.) Müll. Arg.	7	P-S-Aut
Sebastiania commersoniana (Baill.) L.B.Sm. & Downs	909	P-M-Aut/Hyd
Sebastiania brasiliensis Spreng.	43	Ld-M-Aut
Myrtaceae		

Eugenia schuechiana Berg	17	St-S-Zoo
Myrcia selloi (Spreng) N.Silveira	4	Ld-M-Zoo
Eugenia uniflora L.	168	Ld-M-Zoo
Eugenia uruguayensis Cambess.	124	Ld-M-Zoo
Myrciaria tenella (DC.) Berg	23	Ld-S-Zoo
Eugenia involucrata DC.	69	Ld-M-Zoo
Eugenia ramboi Legrand	444	St-M-Zoo
Campomanesia xanthocarpa Berg	31	St-M-Zoo
Myrcianthes pungens Berg	15	Ld-M-Zoo
Myrcia glabra (Berg) Legrand	16	St-M-Zoo
Eugenia hiemalis Cambess.	158	Ld-S-Zoo
Calypthrantes conccina DC.	2	St-M-Zoo
Blepharocalyx salicifolius (Kunth) Berg	1	Ld-M-Zoo
Myrcia multiflora (Lam.) DC.	1	Ld-M-Zoo
Sapotaceae		
Chrysophyllum gonocarpum (Mart. & Eichler) Engl.	9	St-M-Zoo
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	101	Ld-M-Zoo
Pouteria gardneriana (DC.) Radlk.	58	P-M-Zoo
Sideroxylum obtusifolium (Roem. & Schult.) Penn.	3	Ld-T-Zoo
Rubiaceae		
Guettarda uruguensis Cham. & Schltdl.	76	P-S-Zoo
Chomelia obtusa Cham. & Schltdl.	74	Ld-S-Zoo
Psychotria carthagenensis Jacq.	1	St-S-Zoo
Faramea montevidensis Cham.	27	St-M-Zoo
Randia ferox (Cham. & Schltdl.) DC.	20	P-S-Zoo
Salicaceae		
Casearia sylvestris Sw.	413	Ld-M-Zoo
Casearia decandra Jacq.	123	St-M-Zoo
Banara tomentosa Clos	15	Ld-M-Zoo
Xylosma pseudosalzmanii Sleumer	3	St-M-Zoo
Xylosma sp.	1	-

Sapindaceae		
Matayba elaeagnoides Radlk.	106	Ld-T-Zoo
Allophylus edulis (A. St-Hil. et al.) Radlk.	147	Ld-M-Zoo
Cupania vernalis Cambess.	492	Ld-M-Zoo
Moraceae		
Sorocea bonplandii (Baill.) W.C. Burger, Lanj. & Boer	280	St-S-Zoo
Ficus luschnathiana (Miq.) Miq.	21	Ld-T-Zoo
Boraginaceae		
Cordia americana (L.) Gottschling & J.E.Mill.	171	Ld-T-Ane
Polygonaceae		
Ruprechtia laxiflora Meisner	103	Ld-T-Ane
Coccoloba cordata Cham.	1	P-M-Zoo
Annonaceae		
Rollinia salicifolia Schltdl.	53	Ld-M-Zoo
Lauraceae		
Ocotea pulchella (Nees) Mez	28	Ld-M-Zoo
Ocotea puberula (Rich.) Nees.	18	Ld-M-Zoo
Nectandra megapotamica	9	Ld-M-Zoo
Myrsinaceae		
Myrsine coriacea (Sw.) R. Br.	12	P-M-Zoo
Myrsine lorentziana (Mez) Arechav.	29	P-M-Zoo
Myrsine loefgrenii (Mez) Otegui	6	P-M-Zoo
Myrsine laetevirens	1	P-S-Zoo
Malvaceae		
Luehea divaricata Mart. & Zucc.	244	P-T-Ane
Meliaceae		
Trichilia elegans Juss.	42	St-S-Zoo
Cabralea canjerana (Vell.) Mart.	56	Ld-E-Zoo
Cedrela fissilis Vell.	1	Ld-E-Zoo
Trichilia claussenii DC.	12	St-M-Zoo
Loganiaceae		

Strychnos brasiliensis (Spreng.) Mart.	19	Ld-M-Zoo
Arecaceae		
Syagrus romanzoffiana (Cham.) Glassm.	14	Ld-T-Zoo
Phytolaccaceae		
Phytolacca dioica L.	2	Ld-T-Zoo
Seguieria aculeata Jacq.	1	Ld-M-Ane
Cannabaceae		
Celtis iguanaea (Jacquin) Spreng.	12	Ld-M-Zoo
Rhamnaceae		
Scutia buxifolia Reissek	7	Ld-M-Zoo
Bignoniaceae		
Jacaranda micrantha Cham.	14	Ld-E-Ane
Tabebuia heptaphylla (Vell.) Toledo	8	Ld-T-Ane
Lamiaceae		
Vitex megapotamica (Spreng.) Mold.	16	Ld-M-Zoo
Solanaceae		
Solanum sanctaecatharinae Dunal	5	Ld-M-Zoo
Anacardiaceae		
Lithrea brasiliensis March.	4	Ld-M-Zoo
Ebenaceae		
Diospyros inconstans Jacq.	23	Ld-M-Zoo
Celastraceae		
Maytenus dasyclada Mart.	12	St-S-Zoo
Maytenus aquifolia Mart.	1	St-E-Zoo
Maytenus muelleri Schwacke	14	Ld-S-Zoo
Rosaceae		
Prunus myrtifolia (L.) Urban	2	Ld-M-Zoo
Asteraceae		
Gochnatia polymorpha Cabr.	1	Ld-M-Ane
Symplocaceae		
Symplocos lanceolata (Mart.) DC.	4	Ld-M-Zoo

Symplocos uniflora (Pohl) Benth.	12	Ld-M-Zoo
Rutaceae		
Zanthoxylum fagara (L.) Sarg.	1	Ld-M-Zoo
Helietta apiculata Benth.	1	Ld-M-Ane
Zanthoxylum rhoifolium (L.) Sarg.	2	Ld-M-Zoo
Verbenacease		
Cytharexylum montevidense (Spreng.) Mold.	1	Ld-T-Zoo
Simaroubaceae		
Picrasma crenata (Vell.) Engl.	1	St-M-Zoo
Combretaceae		
Terminalia australis Cambess.	27	P-M-Ane/Hid
Proteaceae		
Roupala brasiliensis Klotzsch	2	St-E-Zoo
Thymelaeaceae		
Daphynopsis racemosa Griseb	12	St-S-Zoo
Erythroxylaceae		
Erythroxylum myrsinites Mart.	1	Ld-M-Zoo

Apêndice 2.

Flood levels of each sampling unit across the riparian forest of Rio Botucaraí, Southern Brazil. S.U. = sampling unit; Level = vertical distance of each sampling unit from the river mean level; FF = flood frequency · year^{-1}.

S.U.	Level	FF
S.U.1	5.33	5.95
S.U.2	6.14	4.52
S.U.3	6.56	3.78
S.U.4	6.5	4.52
S.U.5	6.59	3.78
S.U.6	6.73	3.78
S.U.7	6.67	3.78
S.U.8	6.56	3.78
S.U.9	7.09	3.3
S.U.10	7.8	3.21
S.U.11	5.51	5.04
S.U.12	5.71	5.04
S.U.13	6.04	4.52
S.U.14	6.31	4.52
S.U.15	6.48	4.52
S.U.16	6.56	3.78
S.U.17	6.48	4.52
S.U.18	6.29	4.52
S.U.19	7.21	3.3
S.U.20	7.84	3.21
S.U.21	5.33	5.95
S.U.22	4.8	6.65
S.U.23	5.8	5.04
S.U.24	6.01	4.52
S.U.25	6.1	4.52
S.U.26	6.23	4.52
S.U.27	6.2	4.52
S.U.28	6.36	4.52
S.U.29	7.11	3.3
S.U.30	7.92	3.21
S.U.31	4.98	6.65
S.U.32	4.49	7
S.U.33	5.32	5.95
S.U.34	5.57	5.04
S.U.35	5.88	5.04
S.U.36	6.14	4.52
S.U.37	6.01	4.52
S.U.38	6.35	4.52
S.U.39	7.17	3.3
S.U.40	8.03	3.21
S.U.41	4.3	7
S.U.42	4.18	7
S.U.43	4.89	6.65
S.U.44	5.7	5.04
S.U.45	5.91	5.04
S.U.46	5.98	5.04
S.U.47	5.69	5.04
S.U.48	6.15	4.52
S.U.49	7.21	3.3
S.U.50	8.04	2.6
S.U.51	4.14	7.04
S.U.52	4.06	7.04
S.U.53	5.18	5.95
S.U.54	5.59	5.04
S.U.55	5.55	5.04
S.U.56	5.52	5.04
S.U.57	5.49	5.95
S.U.58	6.21	4.52
S.U.59	7.18	3.3
S.U.60	8.03	2.6
S.U.61	4.09	7.04
S.U.62	4.07	7.04
S.U.63	4.89	6.65
S.U.64	5.07	5.95
S.U.65	5.12	5.95
S.U.66	5.48	5.95
S.U.67	5.54	5.04
S.U.68	6.29	4.52
S.U.69	7.32	3.3

S.U.70	8.09	2.6
S.U.71	3.25	8.39
S.U.72	3.51	7.78
S.U.73	4.39	7
S.U.74	4.66	6.65
S.U.75	4.71	6.65
S.U.76	5.11	5.95
S.U.77	5.03	5.95
S.U.78	6.05	4.52
S.U.79	7.4	3.3
S.U.80	8.08	2.6
S.U.81	3.21	8.39
S.U.82	3.04	8.86
S.U.83	4.17	7
S.U.84	4.42	7
S.U.85	4.48	7
S.U.86	5.17	5.95
S.U.87	5.39	5.95
S.U.88	6.27	4.52
S.U.89	7.36	3.3
S.U.90	8.04	2.6
S.U.91	4.01	7.04
S.U.92	3.93	7.04
S.U.93	4.02	7.04
S.U.94	4.09	7.04
S.U.95	4.76	6.65
S.U.96	5.04	5.95
S.U.97	5.86	5.04
S.U.98	6.14	4.52
S.U.99	7.22	3.3
S.U.100	8.04	2.6
S.U.101	7.13	3.3
S.U.102	6.81	3.78
S.U.103	6.99	3.78
S.U.104	7.11	3.3
S.U.105	7.2	3.3
S.U.106	7.26	3.3
S.U.107	7.01	3.3
S.U.108	6.93	3.78
S.U.109	6.88	3.78
S.U.110	7.04	3.3
S.U.111	7.05	3.3
S.U.112	7.46	3.3
S.U.113	7.73	3.21
S.U.114	7.66	3.21
S.U.115	7.97	3.21
S.U.116	7.93	3.21
S.U.117	7.65	3.21
S.U.118	7.66	3.21
S.U.119	7.13	3.3
S.U.120	6.05	4.52
S.U.121	8.11	2.6
S.U.122	8.17	2.6
S.U.123	8.07	2.6
S.U.124	8.02	2.6
S.U.125	8.12	2.6
S.U.126	8.18	2.6
S.U.127	8.13	2.6
S.U.128	8.11	2.6
S.U.129	7.76	3.21
S.U.130	6.85	3.78
S.U.131	8.01	2.6
S.U.132	8.08	2.6
S.U.133	8.21	2.6
S.U.134	8.28	2.6
S.U.135	8.23	2.6
S.U.136	8.16	2.6
S.U.137	8.12	2.6
S.U.138	8.08	2.6
S.U.139	8.01	2.6
S.U.140	7.97	3.21
S.U.141	7.98	3.21
S.U.142	8.11	2.6
S.U.143	8.23	2.6
S.U.144	8.18	2.6
S.U.145	7.94	3.21
S.U.146	7.93	3.21
S.U.147	7.98	3.21
S.U.148	8.06	2.6
S.U.149	8.17	2.6
S.U.150	8.06	2.6
S.U.151	8.06	2.6
S.U.152	8.14	2.6
S.U.153	7.55	3.21
S.U.154	7.71	3.21
S.U.155	7.69	3.21
S.U.156	7.81	3.21
S.U.157	8.12	2.6
S.U.158	7.58	3.21
S.U.159	6.93	3.78
S.U.160	7.59	3.21
S.U.161	7.28	3.3
S.U.162	7.51	3.21

S.U.163	7.59	3.21
S.U.164	6.85	3.78
S.U.165	6.81	3.78
S.U.166	7.06	3.3
S.U.167	7.15	3.3
S.U.168	6.61	3.78
S.U.169	6.26	4.52
S.U.170	6.3	4.52
S.U.171	6.63	3.78
S.U.172	6.45	4.52
S.U.173	6.34	4.52
S.U.174	6.41	4.52
S.U.175	6.53	3.78
S.U.176	6.56	3.78
S.U.177	6.49	4.52
S.U.178	6.43	4.52
S.U.179	6.48	4.52
S.U.180	6.46	4.52
S.U.181	6.58	3.78
S.U.182	6.4	4.52
S.U.183	6.41	4.52
S.U.184	6.5	4.52
S.U.185	6.48	4.52
S.U.186	6.43	4.52
S.U.187	6.5	4.52
S.U.188	6.41	4.52
S.U.189	6.35	4.52
S.U.190	6.34	4.52
S.U.191	7.28	3.3
S.U.192	7.33	3.3
S.U.193	7.28	3.3
S.U.194	7.18	3.3
S.U.195	7.09	3.3
S.U.196	6.91	3.78
S.U.197	6.81	3.78
S.U.198	6.61	3.78
S.U.199	6.59	3.78
S.U.200	6.63	3.78
S.U.201	8.3	2.6
S.U.202	8.3	2.6
S.U.203	8.2	2.6
S.U.204	8.2	2.6
S.U.205	8.2	2.6
S.U.206	8.3	2.6
S.U.207	8.3	2.6
S.U.208	8.3	2.6
S.U.209	8.4	2.6
S.U.210	8.4	2.6
S.U.211	8.2	2.6
S.U.212	8	2.6
S.U.213	7.6	3.21
S.U.214	7.7	3.21
S.U.215	7.6	3.21
S.U.216	6.9	3.78
S.U.217	6.7	3.78
S.U.218	7	3.3
S.U.219	7.2	3.3
S.U.220	7.5	3.3
S.U.221	9.7	1
S.U.222	9.5	1.78
S.U.223	9.4	1.78
S.U.224	9.3	1.78
S.U.225	8.7	2.17
S.U.226	9	1.78
S.U.227	9	1.78
S.U.228	8.9	2.17
S.U.229	8.8	2.17
S.U.230	8.7	2.17
S.U.231	9.1	1.78
S.U.232	7.7	3.21
S.U.233	9.8	1
S.U.234	10.4	0.47
S.U.235	10.7	0.47
S.U.236	10.5	0.47
S.U.237	10.2	0.47
S.U.238	10	0.47
S.U.239	10	0.47
S.U.240	10.5	0.47
S.U.241	11.8	0.26
S.U.242	11.5	-
S.U.243	11.4	-
S.U.244	11.1	-
S.U.245	11.1	-
S.U.246	10.3	0.47
S.U.247	10.4	0.47
S.U.248	10.1	0.47
S.U.249	9.8	1
S.U.250	9.6	1
S.U.251	11.6	-
S.U.252	11.7	-
S.U.253	12.8	-
S.U.254	14.1	-
S.U.255	15	-

S.U.256	15.6	-
S.U.257	15.9	-
S.U.258	16.1	-
S.U.259	15.6	-
S.U.260	15.6	-
S.U.261	13.5	-
S.U.262	13.4	-
S.U.263	13.3	-
S.U.264	13.5	-
S.U.265	13.5	-
S.U.266	13.9	-
S.U.267	13.1	-
S.U.268	12.8	-
S.U.269	12.5	-
S.U.270	12.2	-
S.U.271	12.4	-
S.U.272	14.1	-
S.U.273	16	-
S.U.274	17.5	-
S.U.275	18.7	-
S.U.276	19.9	-
S.U.277	21.1	-
S.U.278	21.7	-
S.U.279	21.5	-
S.U.280	21.7	-
S.U.281	13.9	-
S.U.282	14.6	-
S.U.283	15.1	-
S.U.284	15.6	-
S.U.285	15.6	-
S.U.286	15.5	-
S.U.287	15.2	-
S.U.288	14.8	-
S.U.289	14.5	-
S.U.290	14.6	-
S.U.291	14.9	-
S.U.292	16	-
S.U.293	16	-
S.U.294	18.6	-
S.U.295	19.6	-
S.U.296	21.6	-
S.U.297	23.1	-
S.U.298	23.6	-
S.U.299	24.1	-
S.U.300	25.2	-
S.U.301	> 25.2	-
S.U.302	> 25.2	-
S.U.303	> 25.2	-
S.U.304	> 25.2	-
S.U.305	> 25.2	-
S.U.306	> 25.2	-
S.U.307	> 25.2	-
S.U.308	> 25.2	-
S.U.309	> 25.2	-
S.U.310	> 25.2	-
S.U.311	> 25.2	-
S.U.312	> 25.2	-
S.U.313	> 25.2	-
S.U.314	> 25.2	-
S.U.315	> 25.2	-
S.U.316	> 25.2	-
S.U.317	> 25.2	-
S.U.318	> 25.2	-
S.U.319	> 25.2	-
S.U.320	> 25.2	-
S.U.321	> 25.2	-
S.U.322	> 25.2	-
S.U.323	> 25.2	-
S.U.324	> 25.2	-
S.U.325	> 25.2	-
S.U.326	> 25.2	-
S.U.327	> 25.2	-
S.U.328	> 25.2	-
S.U.329	> 25.2	-
S.U.330	> 25.2	-
S.U.331	> 25.2	-
S.U.332	> 25.2	-
S.U.333	> 25.2	-
S.U.334	> 25.2	-
S.U.335	> 25.2	-
S.U.336	> 25.2	-
S.U.337	> 25.2	-
S.U.338	> 25.2	-
S.U.339	> 25.2	-
S.U.340	> 25.2	-
S.U.341	> 25.2	-
S.U.342	> 25.2	-
S.U.343	> 25.2	-
S.U.344	> 25.2	-
S.U.345	> 25.2	-
S.U.346	> 25.2	-
S.U.347	> 25.2	-
S.U.348	> 25.2	-

S.U.349	> 25.2	-
S.U.350	> 25.2	-
S.U.351	> 25.2	-
S.U.352	> 25.2	-
S.U.353	> 25.2	-
S.U.354	> 25.2	-
S.U.355	> 25.2	-
S.U.356	> 25.2	-
S.U.357	> 25.2	-
S.U.358	> 25.2	-
S.U.359	> 25.2	-
S.U.360	> 25.2	-
S.U.361	> 25.2	-
S.U.362	> 25.2	-
S.U.363	> 25.2	-
S.U.364	> 25.2	-
S.U.365	> 25.2	-
S.U.366	> 25.2	-
S.U.367	> 25.2	-
S.U.368	> 25.2	-
S.U.369	> 25.2	-
S.U.370	> 25.2	-
S.U.371	> 25.2	-
S.U.372	> 25.2	-
S.U.373	> 25.2	-
S.U.374	> 25.2	-
S.U.375	> 25.2	-
S.U.376	> 25.2	-
S.U.377	> 25.2	-
S.U.378	> 25.2	-
S.U.379	> 25.2	-
S.U.380	> 25.2	-
S.U.381	> 25.2	-
S.U.382	> 25.2	-
S.U.383	> 25.2	-
S.U.384	> 25.2	-
S.U.385	> 25.2	-
S.U.386	> 25.2	-
S.U.387	> 25.2	-
S.U.388	> 25.2	-
S.U.389	> 25.2	-
S.U.390	> 25.2	-
S.U.391	> 25.2	-
S.U.392	> 25.2	-
S.U.393	> 25.2	-
S.U.394	> 25.2	-
S.U.395	> 25.2	-
S.U.396	> 25.2	-
S.U.397	> 25.2	-
S.U.398	> 25.2	-
S.U.399	> 25.2	-
S.U.400	> 25.2	-

Apêndice 3.

Contents of clay, silt and sand from 40 transects surveyed across the riverine forest of rio Btucaraí, Southern Brazil.Flood levels of each sampling unit across the riparian forest of Rio Botucaraí, Southern Brazil. S.U. = sampling unit; X = average; SD = standard deviation; CV: coefficient of variation.

	clay X	clay SD	clay CV	silt X	silt SD	silt CV	sand X	sand SD	sand CV
S.U.1	4,028	0,726	0,180	6,26	1,34	0,214	6,381	1,407	0,220
S.U.2	4,009	0,688	0,171	6,135	1,23	0,200	6,537	1,399	0,214
S.U.3	4,043	0,626	0,154	5,858	1,194	0,203	6,785	1,4	0,206
S.U.4	3,894	0,612	0,157	5,568	1,413	0,253	7,047	1,507	0,213
S.U.5	3,856	0,694	0,179	5,235	1,563	0,298	7,27	1,581	0,217
S.U.6	4,029	0,434	0,107	5,322	1,52	0,285	7,158	1,477	0,206
S.U.7	4,386	0,266	0,060	5,833	0,549	0,094	6,795	0,508	0,074
S.U.8	4,758	0,425	0,089	6,098	1,011	0,165	6,276	1,111	0,177
S.U.9	5,009	0,345	0,068	6,43	0,536	0,083	5,766	0,527	0,091
S.U.10	5,185	0,592	0,114	6,715	0,487	0,072	5,112	1,231	0,240
S.U.11	4,295	0,408	0,094	7,005	1,016	0,145	5,322	1,28	0,240
S.U.12	4,457	0,77	0,172	6,655	1,702	0,255	5,663	1,539	0,271
S.U.13	4,123	0,816	0,197	7,213	1,517	0,210	5,329	1,491	0,279
S.U.14	4,38	0,486	0,110	6,691	0,839	0,125	6,101	0,561	0,091
S.U.15	4,82	0,272	0,056	5,805	0,665	0,114	6,677	0,368	0,055
S.U.16	4,825	0,133	0,027	5,51	0,398	0,072	6,868	0,2	0,029
S.U.17	4,805	0,0904	0,018	5,511	0,192	0,034	6,826	0,070	0,010
S.U.18	5,017	0,185	0,036	5,316	0,212	0,039	6,927	0,123	0,017
S.U.19	5,192	0,397	0,076	4,919	0,579	0,117	7,152	0,237	0,033
S.U.20	5,218	0,443	0,084	4,447	1,065	0,239	7,276	0,266	0,036
S.U.21	13,8	2,251	0,163	66,9	8,412	0,125	18,8	6,303	0,335
S.U.22	13,7	2,71	0,197	61,5	12,895	0,209	21,2	8,6	0,405

S.U.23	15,9	2,767	0,174	59,8	14,046	0,234	23,9	10,17	0,425
S.U.24	14,9	3,929	0,263	61	14,772	0,242	22,3	10,657	0,477
S.U.25	17,1	2,961	0,173	55,8	15,237	0,273	26,7	12,275	0,459
S.U.26	14,6	2,119	0,145	63,9	9,303	0,145	21,7	7,196	0,331
S.U.27	16,9	2,132	0,126	58,7	12,084	0,205	26,1	9,386	0,359
S.U.28	15,1	1,792	0,118	65,3	2,71	0,041	18,5	1,269	0,068
S.U.29	16,2	1,751	0,108	58,9	9,11	0,154	25,9	7,325	0,282
S.U.30	14,9	1,663	0,111	65,2	2,098	0,032	18,8	0,789	0,041
S.U.31	12,8	0,422	0,032	14,4	0,699	0,048	72,5	0,707	0,009
S.U.32	12,8	0,789	0,061	14,9	0,738	0,049	72,8	0,919	0,012
S.U.33	12,7	1,889	0,148	15,7	0,823	0,052	72,3	1,947	0,026
S.U.34	13,5	2,915	0,215	15,6	0,516	0,033	70,6	2,366	0,033
S.U.35	13,5	2,915	0,215	15,1	0,568	0,037	70,4	3,502	0,049
S.U.36	14,3	5,539	0,387	14,8	0,919	0,062	70,6	4,551	0,064
S.U.37	16,4	4,351	0,265	14,9	0,994	0,066	69,2	4,315	0,062
S.U.38	18,3	2,983	0,163	15,7	1,16	0,073	66,5	4,197	0,063
S.U.39	19	4,346	0,228	15,9	1,449	0,091	65,6	5,797	0,088
S.U.40	18,1	4,202	0,232	15,4	1,506	0,097	66,5	5,523	0,083

*Apêndice 4***.**

pH, phosporus (P) and sum of bases (S) from 40 transects surveyed across the riverine forest of rio Btucaraí, Southern Brazil.Flood levels of each sampling unit across the riparian forest of Rio Botucaraí, Southern Brazil. S.U. = sampling unit; X = average; SD = standard deviation; CV: coefficient of variation.

	pH X	**pH SD**	**pH CV**	**P X**	**P SD**	**P CV**	**S X**	**S SD**	**S CV**
S.U.1	4,91	0,152	0,030	6,08	0,587	0,096	15,81	2,303	0,145
S.U.2	4,93	0,177	0,035	5,69	0,955	0,167	15,31	1,876	0,122
S.U.3	4,95	0,196	0,039	5,41	1,093	0,202	15,11	1,358	0,089
S.U.4	4,87	0,189	0,038	5,12	0,771	0,150	15,21	2,332	0,153
S.U.5	4,81	0,202	0,041	5,03	0,469	0,093	14,17	3,749	0,264
S.U.6	4,77	0,189	0,039	5,11	0,844	0,165	12,72	3,36	0,264
S.U.7	4,71	0,179	0,038	5,41	0,94	0,173	13,1	1,798	0,137
S.U.8	4,66	0,212	0,045	6,35	1,563	0,246	13,21	1,215	0,091
S.U.9	4,51	0,238	0,052	7,69	4,262	0,554	12,4	0,847	0,068
S.U.10	4,45	0,28	0,062	7,26	5,645	0,777	11,67	0,717	0,061
S.U.11	4,69	0,16	0,034	5,96	0,862	0,144	7,37	1,502	0,203
S.U.12	4,68	0,225	0,048	6,34	1,41	0,222	6,83	1,587	0,232
S.U.13	4,75	0,288	0,060	7,17	1,158	0,161	6,33	1,348	0,212
S.U.14	4,65	0,165	0,035	6,01	0,956	0,159	7,53	0,817	0,108
S.U.15	4,56	0,069	0,015	5,11	0,664	0,129	8,61	1,79	0,207
S.U.16	4,54	0,069	0,015	4,61	0,491	0,106	8,97	1,378	0,153
S.U.17	4,54	0,069	0,015	4,42	0,461	0,104	8,85	1,756	0,198
S.U.18	4,65	0,085	0,018	4,5	0,51	0,113	9,64	1,09	0,113
S.U.19	4,75	0,143	0,030	4,63	0,799	0,172	10,43	0,753	0,072
S.U.20	4,75	0,165	0,034	4,79	0,692	0,144	10,25	0,412	0,040
S.U.21	4,6	0,125	0,027	6,85	2,93	0,427	5,79	0,719	0,124
S.U.22	5,1	0,548	0,107	7,45	1,125	0,151	10,22	6,256	0,612
S.U.23	4,47	0,125	0,027	6,82	3,213	0,471	5,8	0,871	0,150

S.U.24	5,06	0,372	0,073	7,43	0,879	0,118	11,62	6,106	0,525
S.U.25	4,39	0,166	0,037	5,69	1,864	0,327	4,36	1,109	0,254
S.U.26	5,14	0,227	0,044	6,92	1,328	0,191	12,02	3,551	0,295
S.U.27	4,35	0,178	0,040	5,9	1,404	0,237	4,17	0,806	0,193
S.U.28	5,2	0,115	0,022	6,2	2,15	0,346	12,68	3,786	0,298
S.U.29	4,35	0,158	0,036	6,06	1,089	0,179	3,96	0,425	0,107
S.U.30	5,08	0,162	0,031	5,4	1,793	0,332	10,86	3,069	0,282
S.U.31	4,81	0,331	0,068	6,16	1,517	0,246	2,63	0,999	0,379
S.U.32	4,8	0,368	0,076	5,46	1,941	0,355	2,65	1,067	0,402
S.U.33	4,76	0,35	0,073	6,255	3,367	0,538	2,44	1,486	0,609
S.U.34	4,77	0,327	0,068	6,81	2,627	0,385	2,51	1,543	0,614
S.U.35	4,68	0,239	0,051	7,69	1,568	0,203	2,08	0,839	0,403
S.U.36	4,64	0,165	0,035	9,11	1,794	0,196	1,99	1,106	0,555
S.U.37	4,59	0,145	0,031	8,21	1,886	0,229	1,82	0,719	0,395
S.U.38	4,63	0,245	0,052	6,14	1,63	0,265	2,26	0,685	0,303
S.U.39	4,72	0,22	0,046	5,05	1,054	0,208	3,32	0,832	0,250
S.U.40	4,85	0,151	0,031	4,73	1,068	0,225	3,83	0,847	0,221

Apêndice 5.

Contents of potassium (K), organic matter (OM) and calcium (Ca) from 40 transects surveyed across the riverine forest of rio Btucaraí, Southern Brazil.Flood levels of each sampling unit across the riparian forest of Rio Botucaraí, Southern Brazil. S.U. = sampling unit; X = average; SD = standard deviation; CV: coefficient of variation.

	K X	**K SD**	**K CV**	**OM X**	**OM SD**	**OM CV**	**Ca X**	**Ca SD**	**Ca CV**
S.U.1	65,5	7,028	0,107	1,544	0,2	0,129	10,61	1,577	0,148
S.U.2	69	7,916	0,114	1,604	0,174	0,108	10,63	1,678	0,157
S.U.3	70,9	6,855	0,096	1,574	0,122	0,077	10,14	1,368	0,134
S.U.4	59,9	7,637	0,127	1,514	0,207	0,136	9,57	1,536	0,160
S.U.5	51,6	10,7	0,207	1,518	0,289	0,190	9,59	2,391	0,249
S.U.6	53,4	10,135	0,189	1,54	0,207	0,134	8,35	1,679	0,201
S.U.7	60,1	7,094	0,118	1,646	0,153	0,092	8,54	1,271	0,148
S.U.8	67,3	6,325	0,093	1,707	0,134	0,078	8,68	0,944	0,108
S.U.9	70,5	15,4	0,218	1,729	0,146	0,084	8,16	0,47	0,057
S.U.10	69,6	25,988	0,373	1,747	0,201	0,115	7,78	0,447	0,057
S.U.11	91,3	32,595	0,357	1,472	0,263	0,178	3,16	1,028	0,325
S.U.12	113,2	25,037	0,221	1,56	0,358	0,229	3,2	1,476	0,461
S.U.13	128,8	20,176	0,156	1,461	0,359	0,245	2,67	1,574	0,589
S.U.14	109,7	24,235	0,220	1,777	0,159	0,089	2,96	1,056	0,356
S.U.15	107,3	25,421	0,236	1,989	0,0698	0,035	3,31	0,657	0,198
S.U.16	106	15,839	0,149	2,014	0,0519	0,025	3,77	0,435	0,115
S.U.17	98,7	27,378	0,277	1,965	0,0874	0,044	4,07	0,662	0,162
S.U.18	85,3	17,127	0,200	1,852	0,108	0,058	3,89	0,743	0,191
S.U.19	66,2	14,133	0,213	1,775	0,099	0,055	3,84	1,063	0,276
S.U.20	72,5	10,19	0,140	1,751	0,069	0,039	3,91	1,201	0,307
S.U.21	66,9	8,279	0,123	2,03	0,625	0,307	4,04	0,652	0,161
S.U.22	85,3	8,782	0,102	3,2	1,257	0,392	8,46	5,386	0,636
S.U.23	69,7	13,849	0,198	2,33	0,527	0,226	4,21	0,844	0,200

S.U.24	89,6	12,51	0,139	3,31	1,165	0,351	9,5	5,066	0,533
S.U.25	70,2	10,185	0,145	2,49	0,448	0,179	3,25	0,872	0,268
S.U.26	107,8	23,766	0,220	4,09	0,825	0,201	10,75	3,838	0,357
S.U.27	71,8	10,528	0,146	2,92	0,571	0,195	2,8	0,481	0,171
S.U.28	116,9	34,691	0,296	4,58	0,993	0,216	9,53	2,926	0,307
S.U.29	75,2	12,237	0,162	3,34	0,613	0,183	2,62	0,278	0,106
S.U.30	100,4	27,069	0,269	4,35	0,735	0,168	8,94	2,598	0,290
S.U.31	64,2	23,261	0,362	2,52	0,485	0,192	1,99	0,477	0,239
S.U.32	58,1	18,687	0,321	2,43	0,383	0,157	1,96	0,724	0,369
S.U.33	58,7	19,224	0,327	2,51	0,433	0,172	1,91	1,11	0,581
S.U.34	53	19,636	0,370	2,54	0,602	0,237	2,08	1,359	0,653
S.U.35	52,9	7,992	0,151	2,34	0,822	0,351	1,45	0,758	0,522
S.U.36	57	14,166	0,248	2,47	1,01	0,408	1,35	0,885	0,655
S.U.37	70,6	14,238	0,201	2,77	0,814	0,293	1,25	0,495	0,396
S.U.38	87,9	38,031	0,432	3,01	0,654	0,217	1,44	0,42	0,291
S.U.39	118,8	66,096	0,556	3,57	0,327	0,091	2,15	0,443	0,206
S.U.40	135,7	85,535	0,630	3,73	0,236	0,063	2,64	0,435	0,164

Apêndice 6.

Contents of magnesium (Mg), potential acidity (Al+H) and cation exchange capacity from 40 transects surveyed across the riverine forest of rio Btucaraí, Southern Brazil.Flood levels of each sampling unit across the riparian forest of Rio Botucaraí, Southern Brazil. S.U. = sampling unit; X = average; SD = standard deviation; CV: coefficient of variation.

	Mg X	**Mg SD**	**Mg CV**	**Al+H X**	**Al+H SD**	**AL+H CV**	**CEC-T X**	**CEC SD**	**CEC CV**
S.U.1	4,73	0,66	0,139	9,67	5,813	0,601	25,57	8,002	1,012
S.U.2	4,65	0,669	0,143	8,56	5,186	0,605	24,34	7,245	0,895
S.U.3	4,44	0,746	0,168	7,42	4,39	0,591	23,06	5,943	0,720
S.U.4	4,22	0,905	0,214	9,66	6,821	0,706	24,52	9,731	1,210
S.U.5	4,41	1,341	0,304	11,87	9,563	0,805	26,66	12,514	1,607
S.U.6	3,6	0,629	0,174	11	8,242	0,749	24,08	9,281	1,223
S.U.7	3,91	0,446	0,114	13,47	5,41	0,401	26,7	5,42	0,756
S.U.8	4,25	0,409	0,096	15,15	3,648	0,240	30,35	4,72	0,691
S.U.9	4	0,353	0,088	21,86	6,826	0,312	35,91	8,555	1,357
S.U.10	3,71	0,36	0,097	27,69	11,694	0,422	40,59	11,633	2,039
S.U.11	1,75	0,268	0,153	12,23	4,266	0,348	20,9	4,886	0,814
S.U.12	1,71	0,288	0,168	13	6,532	0,502	19,93	7,86	1,293
S.U.13	1,6	0,267	0,166	10,69	6,46	0,604	16,6	8,227	1,246
S.U.14	1,76	0,165	0,093	9,84	4,991	0,507	17,08	5,146	0,752
S.U.15	2	0,327	0,163	10,18	2,875	0,282	17,69	2,829	0,403
S.U.16	1,83	0,309	0,168	12,57	1,659	0,131	20,86	2,318	0,352
S.U.17	1,76	0,474	0,269	15,14	2,894	0,191	23,74	2,536	0,414
S.U.18	2,13	0,33	0,154	14,72	2,842	0,193	24,42	2,778	0,440
S.U.19	2,39	0,348	0,145	14,97	4,52	0,301	25,15	4,48	0,688
S.U.20	2,41	0,264	0,109	15,03	4,934	0,328	25,54	4,48	0,698
S.U.21	1,16	0,259	0,223	8,06	3,194	0,396	12,19	2,693	0,058
S.U.22	1,97	0,855	0,434	5,15	2,486	0,482	18,23	4,697	0,071

S.U.23	1,13	0,333	0,294	9,09	2,894	0,318	14,46	2,57	0,072
S.U.24	2,11	0,761	0,360	5,22	1,864	0,357	17,96	4,272	0,066
S.U.25	0,99	0,269	0,271	11,59	3,522	0,303	16,47	3,591	0,144
S.U.26	2,1	0,645	0,307	5,5	1,113	0,202	17,74	3,202	0,047
S.U.27	1,04	0,207	0,199	13,3	5,648	0,424	17,58	5,575	0,235
S.U.28	2,09	0,569	0,272	6,01	1,576	0,262	18,37	3,025	0,044
S.U.29	1,01	0,11	0,108	12,59	4,392	0,348	16,67	4,509	0,196
S.U.30	1,86	0,425	0,228	7,52	2,28	0,303	18,11	1,8	0,029
S.U.31	0,81	0,218	0,269	5,56	0,744	0,133	8,54	0,916	0,032
S.U.32	0,76	0,267	0,351	5,4	0,62	0,114	8,24	0,888	0,032
S.U.33	0,66	0,372	0,563	5,25	0,57	0,108	7,95	1,213	0,046
S.U.34	0,65	0,372	0,572	5,2	0,587	0,112	8,26	1,345	0,062
S.U.35	0,59	0,288	0,488	5,41	0,956	0,176	8,05	1,958	0,085
S.U.36	0,56	0,232	0,414	5,47	1,669	0,305	7,57	2,442	0,096
S.U.37	0,56	0,165	0,294	6,22	2,09	0,336	9,01	2,722	0,108
S.U.38	0,67	0,302	0,450	7,61	3,005	0,394	10,42	2,71	0,112
S.U.39	0,9	0,17	0,188	7,66	1,957	0,255	11,18	2,139	0,065
S.U.40	1,07	0,116	0,108	6,89	1,371	0,198	11,12	1,259	0,033

*Apêndice 7***.**

Saturation of bases (V), average elevation (E) and flooding frequency per year (FF) from 40 transects surveyed across the riverine forest of rio Btucaraí, Southern Brazil.Flood levels of each sampling unit across the riparian forest of Rio Botucaraí, Southern Brazil. S.U. = sampling unit; X = average; SD = standard deviation; CV: coefficient of variation.

	V X	**V SD**	**V CV**	**E X**	**E SD**	**E CV**	**FF X**	**FF SD**	**FF CV**
S.U.1	7,902	0,626	0,079	6,597	0,627	0,095	4,04	0,795	0,196
S.U.2	8,091	0,689	0,085	6,443	0,68	0,105	4,297	0,649	0,151
S.U.3	8,254	0,648	0,078	6,186	0,865	0,139	4,675	1,044	0,223
S.U.4	8,039	0,795	0,098	5,994	1,034	0,172	4,975	1,265	0,254
S.U.5	7,787	0,854	0,109	5,805	1,197	0,206	5,123	1,47	0,286
S.U.6	7,583	1,051	0,138	5,695	1,219	0,214	5,152	1,445	0,280
S.U.7	7,169	0,821	0,114	5,596	1,303	0,232	5,404	1,528	0,282
S.U.8	6,827	0,564	0,082	5,219	1,554	0,297	5,879	1,875	0,318
S.U.9	6,302	0,731	0,115	5,155	1,657	0,321	6,057	2,052	0,338
S.U.10	5,704	0,923	0,161	5,311	1,461	0,275	5,622	1,676	0,298
S.U.11	5,996	0,521	0,086	7,036	0,142	0,020	3,492	0,248	0,071
S.U.12	6,075	0,999	0,164	7,429	0,57	0,076	3,368	0,407	0,120
S.U.13	6,6	1,177	0,178	7,952	0,405	0,050	2,779	0,401	0,144
S.U.14	6,843	0,982	0,143	8,115	0,104	0,012	2,661	0,193	0,072
S.U.15	7,005	0,694	0,099	8,064	0,106	0,013	2,844	0,315	0,110
S.U.16	6,568	0,415	0,063	7,718	0,358	0,046	3,084	0,377	0,122
S.U.17	6,111	0,623	0,101	6,942	0,463	0,066	3,67	0,507	0,138
S.U.18	6,313	0,4	0,063	6,478	0,0815	0,012	4,298	0,357	0,083
S.U.19	6,51	0,498	0,076	6,44	0,0745	0,011	4,446	0,234	0,052
S.U.20	6,413	0,551	0,085	6,971	0,298	0,042	3,54	0,253	0,071
S.U.21	45,9	9,48	0,206	8,29	0,0738	0,008	2,6	0	0
S.U.22	65,5	17,784	0,271	7,44	0,484	0,065	3,229	0,396	0,122
S.U.23	35,6	9,536	0,267	9,1	0,353	0,038	1,858	0,358	0,192

S.U.24	63,9	18,089	0,283	9,89	0,895	0,090	0,928	0,907	0,977
S.U.25	24,9	11,59	0,465	10,71	0,767	0,071	0,367	0,392	1,068
S.U.26	66,9	12,845	0,192	14,4	1,751	0,121	0	0	0
S.U.27	23,7	8,706	0,367	13,17	0,523	0,039	0	0	0
S.U.28	67,4	6,398	0,094	18,46	3,367	0,182	0	0	0
S.U.29	23	6,218	0,270	14,94	0,558	0,037	0	0	0
S.U.30	60,6	9,348	0,154	20,27	3,777	0,186	0	0	0
S.U.31	28,4	13,235	0,466	15,29	0,708	0,046	0	0	0
S.U.32	27,1	14,004	0,516	16,7	0,392	0,023	0	0	0
S.U.33	26,1	15,751	0,603	17,78	0,567	0,031	0	0	0
S.U.34	21,4	18,02	0,842	18,71	0,475	0,025	0	0	0
S.U.35	23	10,954	0,476	19,69	0,354	0,017	0	0	0
S.U.36	25,4	6,586	0,259	20,4	0,516	0,025	0	0	0
S.U.37	25	4,028	0,161	21,01	0,42	0,019	0	0	0
S.U.38	24,1	8,157	0,338	21,24	0,375	0,017	0	0	0
S.U.39	32,6	6,293	0,193	22,306	0,51	0,022	0	0	0
S.U.40	38	7,134	0,187	22,58	0,637	0,028	0	0	0