



**UNIVERSIDADE FEDERAL DE MINAS GERAIS**  
**INSTITUTO DE CIÊNCIAS BIOLÓGICAS**

Departamento de Botânica

**Programa de Pós-Graduação em Biologia Vegetal**



**DANILO RAFAEL MESQUITA NEVES**

**CONTROLES AMBIENTAIS NA COMPOSIÇÃO  
FLORÍSTICA E NA FILODIVERSIDADE BETA EM  
FLORESTAS SAZONALMENTE SECAS DO DIAGONAL  
SUL-AMERICANO DE FORMAÇÕES ABERTAS**

Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Doutor em Biologia Vegetal.

Área de Concentração: Ecologia e Fisiologia Vegetal

**BELO HORIZONTE – MG**

**2013**



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Área de Concentração: Ecologia e Fisiologia Vegetal

**Orientador: Prof. Dr. Ary Teixeira de Oliveira Filho**  
Universidade Federal de Minas Gerais

**Coorientadora: Dra. Suzana Maria de Salis**  
Embrapa Pantanal

**Orientador no exterior: Dr. R. Toby Pennington**  
Royal Botanic Garden Edinburgh

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Após conversar com o Salsicha, entrei em contato com a professora Denise, que na época era coordenadora do programa de pós em biologia vegetal da UFMG. A mesma me disse que o prazo pra candidatar ao fluxo contínuo estava quase acabando e que eu tinha que correr pra enviar a papelada. No fim deu tudo certo... me inscrevi, comprei minhas passagens pra Belo Horizonte, estudei (muito!) e fiz a seleção. Agradeço a banca examinadora composta pela professora Denise e pelos professores Ary, Pires e Borba, pelas sugestões durante a defesa do meu projeto. Os comentários foram muito construtivos e me fizeram pensar, durante o vôo de volta, em novas abordagens para tentar responder as minhas dúvidas científicas. No final das contas, mudei meu projeto para uma área mais adequada ao conhecimento do Ary: florística, estrutura e biogeografia. Agradeço ao professor Ary, o qual iria se tornar meu orientador, por ter me dado a notícia da aprovação antes do resultado oficial. Eu estava sentado próximo à secretaria da pós, e lembro que este foi, sem dúvida, o momento mais feliz da minha vida, principalmente por causa dos desafios que passei para atingir essa meta. Dedico então, este parágrafo (e outro subsequente) ao professor Ary, por ter prontamente aceito me orientar.

Um pouco depois de receber a notícia da aprovação, desci ao laboratório de Sistemática Vegetal pra conversar com o Ary e pra conhecer as pessoas que iriam conviver comigo nos próximos quatro anos. Me lembro que não encontrei o Ary e que o Daniel Souza me disse que, quando presente, o mesmo ficava de porta aberta. Na ausência do Ary, aproveitei pra fazer contatos em relação à moradia. Conversei com o Marcos “Marquito” Miranda, o qual viria a se tornar um grande amigo. Ele não tinha vaga na república onde morava, mas me passou o email do Eric “japanese”, uma vez que o mesmo era de Uberlândia e, provavelmente, moraria em república. Lembro de enviar email pro Eric perguntando sobre vaga, e descobri que o mesmo morava em pensionato. Mais pra frente descobri também que o Eric não é de Uberlândia, mas sim de Registro, que ama o São Paulo F.C., e que se tornaria meu melhor amigo dentro da pós. Não convivi muito tempo com o japonês, pois eu literalmente não desfiz as malas durante o doutorado, principalmente devido a coletas no Pantanal e ao doutorado sanduíche. No entanto, os poucos momentos que trocamos idéia, bem como os muitos que bebemos trocando idéia, foram bem agradáveis. Infelizmente não pude, por motivos que só fazem sentido na minha cabeça, ir na defesa de doutorado do Japa, e acabei perdendo a apresentação não apenas de um amigo, mas também de um profissional que admiro muito. Por ter sido contemporâneo do Eric, posso dizer que foi um prazer ter sido da turma de doutorado de um amigo que já é, e vai se tornar ainda mais, um cientista brilhante. Dedico então, esse parágrafo ao Japa, pelo companheirismo, aprendizado, algumas bebida (o quê? cerveja), conversas boas durante a viagem pra Uberlândia no início do doutorado e também durante as viagens de campo (Mantiqueira e Minas como um todo).

Após uma busca cansativa, consegui vaga em república que ficava próximo da UFMG. Sendo assim, voltei pra Campo Grande, arrumei as malas, joguei no carro e peguei o trecho pra BH. Este seria o início dos melhores anos da minha vida profissional e pessoal. Morei o primeiro ano com sete pessoas na mesma casa (república Baco): Silvestre, Calouro, Topô (*in memorian*), Pingo, Bruce, Grampola e Herlon. Apesar de parecer muita gente dividindo o mesmo espaço, foi uma época agradável, pois sempre era bom voltar pra casa depois de um dia cansativo e sempre ter amigos pra conversar. Em relação ao trabalho na Sistemática Vegetal, alguns dias eram cansativos, mas nunca estressantes. Posso dizer que nunca me senti tão bem num ambiente de trabalho como na época do doutorado. Almoço de galera seguido de cafézinho e bate-papo agradável era apenas uma das coisas boas de lá. Tinha ainda a festinha com cerveja da última sexta do mês, os dias que a gente descia junto pro buteco da Bio (quando existia), as festas juninas na casa do Pedrinho, Botanical Food Shop na casa do Marquito, as participações/bebedeiras em Congressos (Manaus e Joinville) etc. Destaco ainda o curso de campo no Caparaó, onde coletamos, coletamos, bebemos, coletamos, aprendemos. Um agradecimento especial ao Fredão “doritão”, à Luiza e à Ana Paula, que formaram, juntamente comigo, o grupo dos “incansables”, apelido dado pela sagacidade em coletar plantas no Caparaó. Bom, de forma geral, agradeço a todos que passaram pela Sistemática e fizeram dele um lugar confortável de trabalhar, o que, por sua vez, deixou o ambiente ainda mais produtivo: Aninha, Caetano, Leandro “jácomi” Giacomini, Thaís, Túlio, Mari Bünger, Talita, Érica Borsali, Bruno “Brunífero” Falcão, Suzana, Mari Augsten, Marcelo “salsicha”, Mocotó, Nara, Pedrinho, Pedro Miranda, Vanessa, professor Salino, Gustavo “haregusta” Heringer, Raquel, professor João Renato, Leandro Assis, André “timão”, Aline Joseph, Aline Vale, Bruno Carvalho, Cláudio Nicoletti, Fifão, Francine (Franshine), Izabella, Juliana, Lili, Luiza Fonseca, Maria José,

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## 1. RESUMO GERAL

Estudos que possam auxiliar na conservação de florestas tropicais sazonalmente secas (FTSS) são imprescindíveis, tendo em vista que este bioma encontra-se altamente degradado por ações antrópicas. Um melhor entendimento dos fatores que influenciam a distribuição das espécies no espaço e no tempo é um ponto crítico para subsidiar medidas de conservação em ambientes ameaçados, o que, portanto, justificou avaliar os controles ambientais sobre a variação florística e filogenética de FTSS do diagonal sul-americano de formações abertas (diagonal seco). A partir de um banco de dados que consistiu de 282 inventários florísticos e 36 variáveis ambientais, nós investigamos os efeitos de fatores espaciais e ambientais sobre os padrões de *turnover* florístico e filogenético de FTSS do diagonal seco, utilizando métodos de partição de variância, regressões lineares e análises multivariadas. Nossos resultados demonstraram que os controles ambientais, previamente negligenciados por outros autores, são fatores significativos que influenciam a variação na composição florística e no *turnover* filogenético de FTSS. Estes resultados apontam para três principais considerações: (1) é inapropriado considerar os fatores espaciais como os únicos responsáveis pela variação na composição de espécies de FTSS; (2) devido à alta congruência entre *turnover* florístico e variação ambiental em FTSS, recomenda-se a utilização de variáveis climáticas para definição de ecorregiões, até que listas florísticas eficientes estejam disponíveis para tal função; e (3) considerando nossa demonstração de controles ambientais sobre o *turnover* filogenético, enfatizamos a importância de estudos para a compreensão do efeito das flutuações climáticas em FTSS, devido principalmente ao alto grau de ameaça dessas formações e somado a um possível cenário de mudança climática global.

**Palavras-chave:** diagonal seco da América do Sul, heterogeneidade climática, partição de variância, *turnover* filogenético, diversidade beta, unidades de conservação.

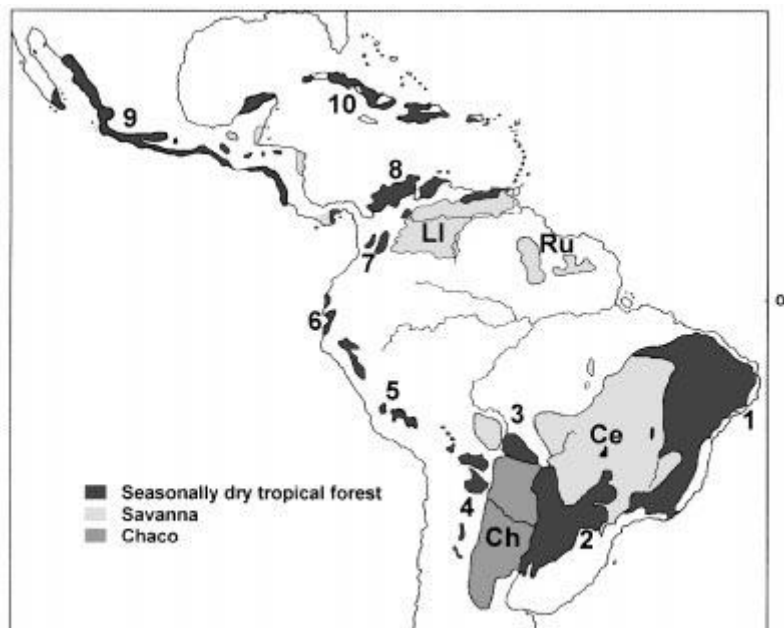
## 2. GENERAL ABSTRACT

Studies that may aid the conservation of seasonally dry tropical forests (SDTFs) are urgently needed, since this biome has been highly threatened by anthropic actions. A better understanding of the factors driving the distribution of species across space and through time is critical to support conservation strategies in threatened environments, which therefore justified our reasons to test whether environmental conditions are important factors affecting the floristic and phylogenetic turnover (phylobetadiversity) in SDTFs of the South American Diagonal of Open Formations (Dry Diagonal). Using a database that consisted of 282 SDTFs and 36 environmental variables, we assessed the relative contribution of spatial and environmental factors in explaining the community composition variation and the phylobetadiversity in SDTFs of the Dry Diagonal, applying variance partitioning methods, distance modelling and multivariate analyses. Our results showed that environmental controls, which were previously neglected by other authors, are significant factors affecting both the floristic and the phylogenetic turnover in SDTFs. These results point to three main considerations: (1) it is inappropriate to consider the spatial factors as the only drivers of variation in species composition in SDTFs; (2) given the high congruence between floristic turnover and environmental variation in SDTFs, using environmental data to define ecoregions is recommended, until effective floristic lists become available for such purpose; and (3) considering our results of environmental conditions driving the phylobetadiversity, and taking into account a possible scenario of global climatic change, we emphasize the importance of studies that aim to understand the effect of climatic fluctuations in SDTFs.

**Key-words:** South American Dry Diagonal, climatic heterogeneity, variance partitioning, phylogenetic turnover, beta diversity, conservation units.

### 3. INTRODUÇÃO GERAL

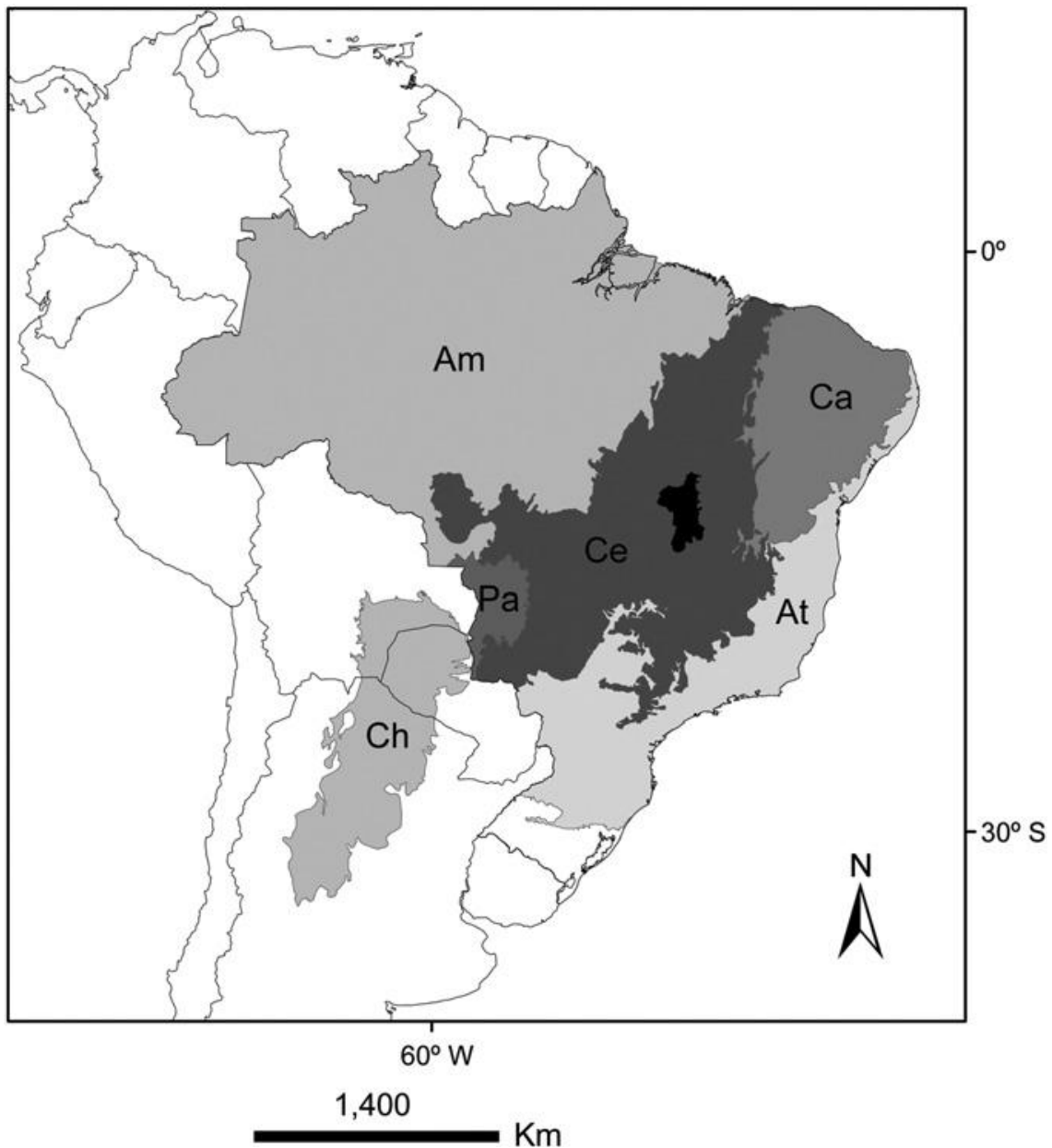
As florestas tropicais sazonalmente secas ocorrem de forma disjunta ao longo da América Latina, do noroeste mexicano ao norte da Argentina e nordeste do Brasil (Figura 1) (PENNINGTON *et al.*, 2006). Estas florestas fazem parte de um bioma mundialmente conhecido como *seasonally dry tropical forests* (SDTFs), o qual é macroclimaticamente delimitado por (1) precipitação média anual menor que 1600 mm; (2) estação seca marcante, na qual chove menos de 100 mm por um período de cinco a seis meses; e (3) altas taxas de deciduidade foliar durante a estação seca, período no qual estas formações perdem mais de 50% da massa foliar (BULLOCK *et al.*, 1995; GENTRY, 1995; PENNINGTON *et al.*, 2000; 2009; OLIVEIRA-FILHO, 2009).



**Figura 1.** A distribuição de formações sazonalmente secas no Neotrópicos. Florestas tropicais sazonalmente secas; 1, Caatinga. 2, Núcleo Misiones. 3, Região dos Chiquitanos. 4, Núcleo Piedmont. 5, Vales interandinos da Bolívia e Peru. 6, Costa do Pacífico e Equador. 7, Vales interandinos da Colômbia. 8, Costa caribenha da Colômbia e Venezuela. 9, América Central. 10, Antilhas. Savanas: Ce, Cerrado. Ll, Llanos. Ru, Rupununi. Ch, Chaco. Modificado de PENNINGTON *et al.* (2000), com permissão.

O maiores núcleos de SDTFs encontram-se no diagonal sul-americano das formações abertas (também conhecido como diagonal seco), o qual engloba três principais domínios fitogeográficos: (1) Caatinga, no nordeste brasileiro, uma região de clima semi-árido, secas intensas e baixa sazonalidade térmica; (2) Cerrado, no Brasil

Central, uma região com baixa sazonalidade da precipitação; e (3) Chaco, no norte da Argentina, sul do Paraguai e na porção oeste do estado de Mato Grosso do Sul, as quais são regiões de clima semi-árido, secas intensas e alta sazonalidade térmica (PENNINGTON *et al.*, 2000). As SDTFs deste diagonal seco são encontradas em cinco núcleos principais: (1) Caatinga, o mais extenso; (2) Misiones, que consiste dos baixos cursos dos rios Paraguai e Paraná, bem como do alto curso do rio Uruguai; e (3) Piedmont, que se estende ao longo das montanhas subandinas do nordeste argentino (PRADO & GIBBS, 1993). Ainda, manchas menores também são encontradas de forma disjunta no Cerrado, em áreas de solos férteis; (5) além de intrusões ao longo da borda do Chaco (Figura 2) (RATTER *et al.*, 1988).



**Figura 2.** Localização georreferenciada do diagonal das formações abertas (Ce – Cerrado, Ch – Chaco, e Ca – Caatinga) em relação aos domínios fitogeográficos úmidos (Amazônia – Am e Mata Atlântica – At). Destaque para as regiões do Pantanal (Pa) e do vale do rio Paran (mancha preta), as quais são importantes enclaves de florestas tropicais sazonalmente secas no Brasil Central. Modificado de WERNECK (2011).

Vale ainda ressaltar que no Cerrado e Chaco, as SDTFs esto distribudas em mosaico com os cerrades e as florestas (ou bosques) chaquenhas, as quais so, respectivamente, as principais formaes florestais destes domnios fitogeogrficos (RATTER *et al.*, 1988; PRADO, 1993a,b). Os cerrades so fisio-nomicamente diferentes das SDTFs e, geralmente, ocorrem em solos distrficos, com pH baixo e alto teor de alumnio (RATTER *et al.*, 1988). Alm disso, ao contrrio das espcies de

SDTFs, muitas espécies de cerrado possuem adaptações importantes para tolerância ao fogo (RATTER *et al.*, 1988; PENNINGTON *et al.*, 2000; SIMON & PENNINGTON, 2012). As florestas chaquenhass, por sua vez, são fisionomicamente parecidas com as SDTFs, porém floristicamente dissimilares. PENNINGTON *et al.* (2000) relacionam esta alta dissimilaridade à alta sazonalidade climática no Chaco, cujo clima pode variar desde máximas de 50° C no verão chuvoso, até geadas intensas durante o inverno seco. Esta baixa isothermalidade cria um ambiente inóspito para muitas espécies de outros biomas, tendo em vista que as características do solo podem variar de pouco úmido, na estação seca, à encharcado/alagado, durante a estação chuvosa (PRADO, 1993a,b). Somado à estas características edáficas restritivas, algumas regiões chaquenhass possuem ainda solos salinos devido à intrusões oceânicas durante o Mioceno (PENNINGTON *et al.*, 2000).

Devido à uma teoria controversa, as SDTFs, principalmente as inseridas no diagonal seco, têm recebido uma atenção especial de muitos biogeógrafos (e.g., MOONEY *et al.*, 1995; PENNINGTON *et al.*, 2006; 2009; DIRZO *et al.*, 2011). A teoria do arco pleistocênico (TAP), proposta por PRADO & GIBBS (1993), sugere que as atuais manchas disjuntas de SDTFs constituem os remanescentes de uma formação contínua que foi amplamente distribuída pela América do Sul durante o último glacial máximo (~ 21 thousand years BP). A TAP hipotizou que esta formação contínua teria estendido desde o nordeste brasileiro até o sul do Paraguai, norte da Argentina e, potencialmente, até os vales secos interandinos, tendo como base espécies filogeneticamente distantes que foram, no entanto, registradas como amplamente distribuídas nas manchas disjuntas de SDTFs do diagonal seco (PRADO & GIBBS, 1993; PENNINGTON *et al.*, 2000). Entretanto, os estudos subsequentes rejeitam a TAP, mostrando que as espécies que embasaram a hipótese de PRADO & GIBBS



(1993) representam uma pequena minoria (< 2%), e que na verdade a variação florística entre as SDTFs neotropicais (diversidade beta) é mais alta do que esperado ao acaso (e.g., GILLESPIE *et al.*, 2000; TREJO & DIRZO, 2002; LINARES-PALOMINO, 2006; LOTT & ATKINSON, 2006; QUEIROZ, 2006; PENNINGTON *et al.*, 2006; CASTILLO-CAMPOS *et al.*, 2008; LINARES-PALOMINO *et al.*, 2011).

Na tentativa de compreender o que afeta os padrões de diversidade beta em SDTFs, os pesquisadores têm focado as explicações na teoria de biogeografia de ilhas, associando a variação florística com a distância geográfica entre as áreas fonte e as áreas fundadoras (e.g., PENNINGTON *et al.*, 2006; 2009). Dado a configuração disjunta e fragmentada das SDTFs, autocorrelacionar os padrões de diversidade beta com espaço parece ser uma ideia atrativa. No entanto, estes estudos negligenciaram a possibilidade de controles ambientais (clima e solo) na composição de espécies, o que impossibilita um entendimento mais completo sobre a biogeografia destas formações. ter STEEGE *et al.* (2006), por exemplo, demonstraram a importância de clima e solo para explicar o *turnover* florístico entre comunidades de florestas na Amazônia. Entretanto, esta abordagem ainda não foi utilizada para avaliar se o ambiente influencia na variação da composição florística entre SDTFs.

Além da escala espacial, os controles ambientais também podem ser analisados em escalas temporais (GRAHAM & FINE, 2008). Esta metodologia é conhecida como filodiversidade beta, a qual mede como as relações filogenéticas mudam através do espaço, fornecendo assim uma abordagem evolutiva para avaliar as variações nas comunidades vegetais em gradientes ambientais e/ou espaciais. No caso de gradientes ambientais, o *turnover* de clados inteiros indica que o conservatismo de nicho contribuiu para os padrões de composição de espécies observados nas comunidades (GRAHAM & FINE, 2008; ANACKER & HARRISON, 2012). Portanto, analisar o

comprimento dos nichos pode fornecer importantes contribuições para conservação, uma vez que os resultados permitem inferir sobre o efeito que as flutuações climáticas teriam nas diferentes comunidades vegetais.

Medidas que forneçam subsídios à conservação de SDTFs são essenciais, tendo em vista que o bioma, como um todo, encontra-se altamente degradado por ações antrópicas (MILES *et al.*, 2006). No diagonal seco, com o atual nível de expansão agrícola, as SDTFs têm sido rapidamente suprimidas, uma vez que seus solos são, em geral, mais férteis do que o de outras formações (RATTER *et al.* 1988). Além disso, a degradação em SDTFs também é causada por mineradoras (para retirada de calcário), incêndios florestais de origem antrópica, construções de rodovias e ocupação urbana mal planejada (LIMA *et al.*, 2010). Este grau de fragmentação, somado à falta de conhecimento sobre a biogeografia destas formações e como as mesmas reagiriam em um possível cenário de mudança climática, são os pontos mais críticos para a conservação das populações de plantas associadas a ambientes sazonalmente secos, o que justifica avaliar os controles ambientais na composição florística e no *turnover* filogenético de SDTFs do diagonal seco.

Sendo assim, o presente trabalho teve como objetivo principal analisar os controles ambientais na variação da composição florística e na filodiversidade beta em florestas sazonalmente secas do diagonal sul-americano das formações abertas. Ao longo dos capítulos foram testadas três hipóteses:  $H_1$ : a variação na composição de espécies é fortemente ligada à heterogeneidade ambiental (GRAHAM & FINE, 2008), e portanto a filodiversidade beta será positivamente relacionada com o *turnover* florístico.  $H_2$ : a filodiversidade beta é influenciada pelas regras da teoria de biogeografia de ilhas, tais como as grandes distâncias entre as áreas fonte e as áreas fundadoras, e com isso a mesma será relacionada com proximidade geográfica.  $H_3$ : a filodiversidade beta é

determinada por conservatismo de nicho e, portanto, a mesma terá valores maiores quando a variação ambiental for maior.

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**5. CAPÍTULO UM** - Environmental and historical controls on floristic composition  
across the South American Dry Diagonal

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# Environmental and historical controls on floristic composition across the South American Dry Diagonal

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## ABSTRACT

**Aim** To test the role of spatially autocorrelated processes such as environmental factors, historical fragmentation and dispersal limitation, in driving variation in floristic composition across seasonally dry tropical forests (SDTFs) in eastern South America.

**Location** SDTFs extending from the Caatinga of northeastern Brazil to the Chaco of northern Argentina, an area referred to as the “Dry Diagonal”.

**Methods** We compiled a database of 282 inventories of woody vegetation in SDTFs from across the Dry Diagonal and combined this with data for 35 environmental variables. We assessed the relative contribution of spatial and environmental factors in explaining floristic turnover in SDTFs across the Dry Diagonal using variance partitioning methods. In addition we used multivariate analyses to determine which environmental factors might be most important in explaining variation in the composition of SDTF tree communities.

**Results** We found that spatially autocorrelated factors explain 5.5% of the variance in species composition, independent of environmental factors, while environmental factors explain 4.5% independent of space, and spatially-structured environmental factors explains 23.5% of the variation; 66.8% of variation remains unexplained. The main axis of species composition variation is strongly correlated with a north-south gradient in temperature regime. At the extreme south of the Dry Diagonal, this temperature effect appears to underlie floristic similarities between Chaco and southern SDTFs, both of which experience frosts.

**Main conclusions** Historical fragmentation and isolation alone cannot explain the turnover in species composition among these SDTFs as assumed by previous authors. Our results show that environmental factors play an important role in driving floristic variation across the Dry Diagonal. This compositional and environmental heterogeneity needs to be taken into account both to understand the past distribution of SDTF and to effectively manage and conserve this key tropical biome in the face of anthropogenic degradation and global climate change.

### Keywords

**Seasonally dry tropical forests, Pleistocene Arc Hypothesis, Diagonal of Open Formations, species turnover, environmental niche, Chaco, variance partitioning**



## INTRODUCTION

Seasonally dry tropical forests (SDTFs) occur as fragments of varying size throughout Latin America, from Northern Argentina and Northeast Brazil to Northwest Mexico (Pennington *et al.*, 2006). These SDTFs comprise a recognized biome (Pennington *et al.*, 2000; 2009), which is characterized by < 1600 mm precipitation/year, a marked dry season of 5-6 months, and high rates of deciduousness during the dry season (Bullock *et al.*, 1995; Gentry, 1995; Oliveira-Filho, 2009). SDTFs have garnered increased attention in recent years due both to their highly threatened status (e.g. Mooney *et al.*, 1995; Pennington *et al.*, 2006; 2009; Dirzo *et al.*, 2011) as well as because of the influential Pleistocene Arc Hypothesis (PAH; Prado & Gibbs, 1993; Pennington *et al.*, 2000) about their biogeography. The PAH postulated that SDTFs had a more widespread and contiguous distribution in South America during Pleistocene glaciation phases, including areas that are currently covered by rain forest or savanna. The PAH is based upon the widespread distributions of unrelated tree species in disjunct SDTF areas from northeast Brazil through central and southern Brazil to Paraguay and Argentina and in some cases, as far as the dry inter-Andean valleys of western South America. The putative Pleistocene Arc – a more continuous area of SDTF - was suggested to have connected these areas during cooler and drier climates during Pleistocene glaciations (Prado & Gibbs 1993; Pennington *et al.* 2000).

Subsequent research, however, has shown that these widespread species represent a small minority of SDTF tree species and that floristic variation amongst SDTF sites across the Neotropics is high (e.g. Gillespie *et al.*, 2000; Trejo & Dirzo, 2002; Linares-Palomino, 2006; Lott & Atkinson, 2006; Queiroz, 2006; Pennington *et al.*, 2006; Castillo-Campos *et al.*, 2008, Linares-Palomino *et al.*, 2011). For instance, Linares-Palomino *et al.* (2011) showed that less than 2% of 3839 SDTF tree species are found in 10 or more of 21 disjunct SDTF nuclei across the Neotropics. On the other

hand, these authors found lower dissimilarity ( $< 0.75$ ) amongst SDTF nuclei in Brazil and southern South America and suggested that this might offer some support for the idea that SDTF may have been more widespread and continuous within this region during Pleistocenic glacial phases.

When explaining the disjunct distributions of SDTF species, and floristic variation of SDTFs in general, these recent studies have focused primarily on the role of historical biogeographic processes, namely habitat fragmentation and dispersal limitation (e.g. Pennington *et al.*, 2006, 2009). Environmental factors are also expected to affect species' distributions, but no study to date has examined the role of environmental determinants, such as climate, in shaping the distribution of tree species across a large expanse of Neotropical SDTF sites (e.g. across eastern South America).

We aimed to test the role of historical fragmentation and dispersal limitation versus environmental factors in driving floristic differentiation amongst SDTFs. Understanding the roles of these two processes is an important and unsolved issue in many systems (e.g. in the Amazon, Haffer, 1969; ter Steege, 2006; in the Cerrado, Werneck *et al.*, 2012; in South American subtropical forests, Oliveira-Filho *et al.*, 2013). Variance partitioning methods offers a way forward to assess the relative contribution of spatial and environmental factors in driving species turnover (Legendre *et al.*, 2012), but such approach has mostly been used at small spatial scales (e.g. within plots, Legendre *et al.*, 2009) to address the influence of steady-state small scale dispersal limitation. However, it can also be used at much broader scales, as we do here, to address habitat fragmentation and isolation on historical timescales, and may be particularly useful in ecosystems with limited paleoecological data, such as SDTFs.

In this paper, we compiled a database of SDTF floristic inventories from sites extending from the caatinga woodlands of northeastern Brazil to the chaco woodlands

of northern Argentina, an area we refer to as the ‘Dry Diagonal’, following Prado & Gibbs (1993) (also see Vanzolini 1963; Werneck *et al.*, 2012). This region is particularly appropriate because it was the main area studied by Prado & Gibbs (1993) in the development of the PAH and because it has been the target of previous studies on SDTF biogeography (Andrade-Lima, 1954; 1982; Ratter *et al.*, 1988; Caetano & Nasciri, 2011; Werneck *et al.*, 2011; Collevatti *et al.*, 2012; Collevatti *et al.*, 2013a,b). If the floristic variation of SDTFs is due primarily to fragmentation and subsequent dispersal limitation between SDTF patches, then the similarity in species composition of SDTF communities should depend on the distance between them and spatial vectors should explain a large proportion of the variation in community composition. Alternatively, if previously unrecognized environmental conditions within SDTFs are the principal factors driving floristic turnover, then climatic and edaphic variables should explain a large proportion of variation in community composition.

## **METHODS**

### **Study area**

The Dry Diagonal stretches from NE Brazil to Argentina, Paraguay and Bolivia, and occurs primarily in three Phytogeographic Domains which are named after the main vegetation types that occur within them (IBGE, 1993): Caatinga (tropical semi-arid thorn-woodlands), Cerrado (seasonal woody savannas) and Chaco (subtropical/tropical semi-arid thorn-woodlands) (Fig. 1). Prado and Gibbs (1993) defined three major nuclei of SDTF in the Dry Diagonal: 1) the Caatinga Nucleus, which occurs in northeastern Brazil and is the largest Nucleus (essentially the same area as the Caatinga Domain); 2) the Misiones Nucleus, which extends from the lower course of the Paraguay and Paraná rivers to the upper Uruguay River in Misiones, Argentina; and 3) The Piedmont

Nucleus, which occurs along the eastern base of the Andes in north-eastern Argentina. Scattered patches of SDTFs also occur in the Bolivian Chiquitanos (Linares-Palomino *et al.* 2011) and throughout the Cerrado Domain (Ratter *et al.*, 1988; Pennington *et al.*, 2000) on areas of fertile soils.

One environmental element in the definition of SDTFs is that they are a frost-free vegetation (Prado, 1993a,b; Pennington *et al.*, 2000) and regular winter frost is one factor that differentiates the chaco woodlands, found in northern Argentina, western Paraguay, south-eastern Bolivia, and the extreme western edge of Mato Grosso do Sul state in Brazil, from SDTF. However, large areas delimited as SDTF in the schematic maps of previous studies (e.g. Piedmont and Misiones, Prado & Gibbs 1993; Oliveira Filho *et al.*, 2006; Pennington *et al.*, 2009) also receive significant frost (see Results section). Thus, because the exact definition of SDTF, and whether or not it receives significant frost, merits further attention in the future, we chose to include the chaco woodlands in our analyses, since they fit some other criteria of SDTF established by the aforementioned authors, such as seasonality of rainfall and deciduousness.

### **The database of SDTFs**

We extracted floristic inventory data from the TreeAtlas database ver. 2.0. This database consists of >2,000 geo-referenced localities for which lists of tree species (trees defined here as woody plants >3 m in height) were compiled from an extensive survey of published and unpublished (e.g. PhD theses) literature. A TreeAtlas site is defined by a single vegetation type contained in a circular area with a 10-km diameter. Therefore, where two or more vegetation types co-occur in one 10km area, there may be two geographically overlapping sites in the TreeAtlas database, each for a distinct vegetation type. The data derive primarily from inventories of woody vegetation (i.e. plots, transects, and vegetation surveys). Surveys of specimens at major herbaria (e.g.

K, NY, E, RB, BHCB, UEC, SP) are then used to augment the lists for each location with any tree species that were collected within the 10-km diameter of the original TreeAtlas site, and within the same vegetation type. TreeAtlas does not include occurrence records without indication or evidence of vegetation type, and sites with clearly incomplete species lists. The latter is an important sieve because different sample efforts across sites may bias their descriptive power. The 282 TreeAtlas inventories used in this study comprise 134 SDTF sites from the Caatinga, 14 from the Misiones Nucleus, 5 from the Piedmont Nucleus, 91 from SDTF enclaves scattered throughout the Cerrado Domain, 6 from the Bolivian Chiquitanos and 32 chaco woodland sites from the Chaco Domain. The final species matrix contained presence/absence data for 1765 tree species across 282 SDTF sites, with a total of 25,650 presences (see Figure 1).

The TreeAtlas database also includes altitudinal and environmental data for all sites, derived from multiple sources. Eight variables are related to edaphic substrate: mean, minimum and maximum monthly soil moisture (%), obtained from the International Soil Moisture Network ([www.ipf.tuwien.ac.at/insitu/](http://www.ipf.tuwien.ac.at/insitu/)); prevailing slope and aspect, obtained from CGIAR-CSI (2006); soil fertility (% base saturation, hereafter “V%”), soil coarseness (% sand) and substrate rockiness (% surface of rock outcrops), extracted from a detailed map of soil types produced by EMBRAPA & IBGE (2003) using the RadamBrasil Soil Survey of the 1970s and 1980s, and additional field studies carried out by both governmental agencies (EMBRAPA & IBGE, 2003). Climatic variables include the mean duration (days) and severity (mm) of water-deficit periods, both extracted from Walter diagrams (Walter, 1985); the 19 bioclimatic variables produced by WorldClim 1.4, a high-resolution (1 km) database of global climate layers created by Hijmans *et al.* (2005); mean frequency of frosts (days), cloud cover (%) and

cloud interception (mm), obtained from gridded datasets produced by Jones & Harris (2008); and three additional variables derived from WorldClim by Zomer *et al.* (2007, 2008): potential and actual evapotranspiration (mm) and an aridity index. A full description with details of protocols for TreeAtlas 2.0 can be found at <http://www.icb.ufmg.br/treetlan>.

### **Analyses of species composition**

We first explored the patterns of similarity in community composition by conducting a hierarchical clustering analysis of all 282 sites. We used Jaccard distance as the dissimilarity metric and unweighted paired groups as the linkage method (McCune & Grace, 2002). We assessed the confidence for each node of the hierarchical cluster using multiscale bootstrapping (Shimodaira, 2004) in the *pvclust* package (Suzuki & Shimodaira, 2011), in the R Statistical Environment (R Development Core Team, 2012). Because singletons (species found at a single site) commonly increase the intrinsic noise without relevant contribution to most analyses (Lepš & Šmilauer, 2003), we excluded the 318 singleton species from this and all subsequent analyses.

We obtained the relative contribution of spatially autocorrelated and measured environmental factors in explaining variation in community composition by following the methods proposed by Dray *et al.* (2012) and Legendre *et al.* (2012). This routine comprises (i) the Hellinger transformation of the binary presence/absence data, which reduces the effect of widespread species; (ii) the preparation of two Redundancy Analyses (RDA), one for species and spatial variables and another for species and environmental variables, which provides  $R^2$  values for each global model; (iii) the compilation of significant spatial and environmental variables through a forward selection procedure (Blanchet *et al.*, 2008); and (iv) the variance partitioning of the community composition matrix with respect to the significant spatial and environmental

variables. This selection method reduces the risk of overparameterization by using the adjusted  $R^2$  of the global model (RDA) as an additional stop criterion (Borcard *et al.*, 2011). As spatial variables, we used Moran's eigenvector maps (MEMs), which represent the diagonalization of a centred spatial weighting matrix (Dray *et al.*, 2012). We tested the significance of the pure spatial (controlled for environmental variation) and pure environmental (controlled for spatial autocorrelation) fractions of the variation partitioning applying a permutation test (999 permutations) for RDA. All variation partitioning analyses were conducted using the *packfor* (Dray *et al.*, 2011), *spacemaker* (Dray, 2010), *spdep* (Bivand, 2012), *tripack* (Gebhardt, 2009) and *vegan* (Oksanen *et al.*, 2012) packages in the R Statistical Environment.

We then performed a Non-Metric Multidimensional Scaling (NMDS) to derive orthogonal eigenvectors representing gradients in floristic variation summarized by each axis, and used *post-hoc* models to further investigate the role of environmental factors in driving variation in community composition. There was negligible stress reduction in adding >2 NMDS axes, and we therefore focused on the first two axes ( $k = 2$ ) for comparisons with environmental variables. We also visually explored the *post-hoc* models by plotting the NMDS axes and the values of the environmental variables in geographic space. The ordination and *post-hoc* analyses were performed in the statistical package *vegan* (Oksanen *et al.*, 2012), applying the *metaMDS* and *envfit* functions, respectively, and the maps were designed using the package *maptools* (Lewin-Koh & Bivand, 2012), both in the R Statistical Environment.

## RESULTS

The hierarchical clustering results were congruent with the previously-defined SDTF nuclei. The classification segregated the 282 sites into two principal groups, hereafter

termed the “northern” and “southern” groups. The northern group consisted of 231 sites from the Caatinga Nucleus, Cerrado Domain and Bolivian Chiquitanos, whereas the southern one corresponded to 51 sites from Misiones and Piedmont Nuclei and the chaco woodlands from the Chaco Domain (Fig. 2). Two chaco woodlands clustered with the northern group (two blue squares in the Cerrado cluster in Fig. 2), and one Cerrado Domain site clustered with the southern group (red square in the Chaco cluster in Fig. 2). In the northern group, the Caatinga sites that occur along the border with Cerrado Domain (defined as arboreal caatinga by Santos *et al.*, 2012) clustered with the sites from the Cerrado Domain (orange squares segregated from the main orange cluster in Fig. 2). The sites from the Bolivian Chiquitanos also clustered with the SDTFs from the Cerrado Domain, suggesting that these Bolivian SDTFs may not be as distinct floristically.

The forward selection procedure retained 30 MEM eigenfunctions for modelling variation in species composition (adjusted  $R^2 = 0.271$ , which is nearly the same as the value for all 263 MEMs without any selection, adjust  $R^2 = 0.272$ ). All the selected MEMs are among the first 100, which represent broad-scale, positive spatial autocorrelation. Regarding environmental variables, the forward selection retained 31 variables for modelling variation in species composition (adjusted  $R^2 = 0.2755$ , which is nearly the same as the value for all 36 environmental variables without any selection, adjust  $R^2 = 0.2768$ ) (Tab. 1). Aspect, cloud interception, maximum temperature of the hottest month, potential evapotranspiration and precipitation of wettest quarter were the excluded environmental variables. The adjusted  $R^2$  proved to be the relevant stop criterion in the forward selection of the MEMs, whereas the significance level  $\alpha$  was the final stop criterion in the selection of the environmental variables. When partitioning the variation explained by these selected spatial and environmental predictors, we found



that spatially autocorrelated factors explain 5.5% ( $P = 0.001$ ) of the variance in species composition, independent of environmental factors, while environmental factors explain 4.5% ( $P = 0.001$ ) independent of space. Spatially-structured environmental factors explain 23.5% of the variation, and 66.8% of variation remains unexplained.

When investigating which environmental variables explain species turnover across the Dry Diagonal, we found that the variation in species composition summarized by the first NMDS axis reveals a large-scale gradient (Fig. 3a), which is strongly correlated with a north-south gradient in mean minimum temperature of the coldest month (*post-hoc*  $R = 0.99$ ;  $P < 0.001$ ) (Fig. 3c). The first NMDS axis is also congruent with a north-south segregation in days of frost (*post-hoc*  $R = -0.97$ ;  $P < 0.001$ ) (dashed black line in Fig. 3a). The mean minimum of the coldest month in southern SDTFs ranges from 0.1°C to 15.4°C, and some southern SDTFs, such as those from the Piedmont Nucleus, can experience up to 18 days of frost. In the northern group, four sites experience up to three days of frost, while the other 227 sites experience none. The first NMDS axis is also correlated with a north-south gradient in annual temperature range (*post-hoc*  $R = -0.98$ ;  $P < 0.001$ ) (Fig. 3e), suggesting that the high seasonality, including both hot summers and winter frosts in the southern group may be a relevant factor driving variation in community composition.

The community composition variation summarized by the second NMDS axis reveals a rainfall gradient, which is strongly correlated with the precipitation of the wettest month (*post-hoc*  $R = 0.97$ ;  $P < 0.001$ ) (Fig. 3d). In fact, the species composition variation summarized by the second NMDS axis is congruent with most of the precipitation-related variables (Tab. 1), segregating a dry group (Caatinga, chaco woodlands and Piedmont) from a wet group (Cerrado SDTFs and Misiones). Furthermore, the second NMDS axis correlates with maximum soil water storage

capacity (*post-hoc*  $R = 0.97$ ;  $P < 0.001$ ) (Fig. 3f), suggesting an interaction between rainfall and soil characteristics in driving the turnover in species composition summarized by this axis.

## DISCUSSION

Our analyses show that climatic and edaphic condition play a significant role in driving floristic variation amongst SDTFs of the South American Dry Diagonal. Because of these environmental effects, it is therefore inappropriate to designate historical fragmentation and dispersal limitation as the only factors shaping species composition in SDTFs. Most of the proportion of variance in species composition that we are able to explain is assigned to spatially structured environmental variation (23.2%), which means that the predictions made by spatial and niche-based models converged. However, considering that the correlations between composition and environmental variables are known to be important to plants (discussed below), we believe that it is more parsimonious to attribute most of the spatially structured environmental variation to niche-based controls (c.f. Legendre *et al.*, 2009).

At a broad scale within the South American tropics, precipitation regime is likely one primary determinant of the presence versus absence of SDTF, and at a much smaller spatial scale (within northeastern and central-western Brazil), Santos *et al.* (2012) found that precipitation regime was the chief factor determining the species composition of SDTF communities. Nevertheless, in analyzing SDTF communities at a larger spatial scale from across the entire Dry Diagonal, we found temperature-related variables to be the most significant factors affecting variation in species composition of SDTFs and chaco vegetation. In agreement with this result, the fundamental division in our clustering analysis was between two geographically segregated groups, with the

northern group experiencing mild temperatures in the coldest month, no frost (except for three sites with  $\leq 3$  days frost/yr), and low annual temperature range compared to the southern group.

This fundamental latitudinal division reflects higher relative frequencies of species of the families Leguminosae, Bignoniaceae, Moraceae and Annonaceae in the warmer northern group, whereas the relative frequencies of species in Lauraceae, Asteraceae and Melastomataceae are higher in the cooler southern group. The higher frequencies of Leguminosae, Bignoniaceae, Moraceae and Annonaceae in the northern group indicate that the northern flora may be comprised primarily of species incapable of coping with freezing temperatures. Punyasena *et al.* (2008) classified these families as temperature-sensitive, since their abundance and richness decrease in low temperatures.

Rainfall regime correlates strongly with the second gradient of species composition, as summarized by the second NMDS axis. The precipitation division reflects that the relative frequencies of Leguminosae, Capparaceae and Polygonaceae are higher in drier areas, whereas the relative frequencies of Rubiaceae, Moraceae, Arecaceae and Annonaceae are higher in wetter areas. The lower frequencies of Rubiaceae, Moraceae, Arecaceae and Annonaceae in the drier nuclei (Caatinga, Chaco and Piedmont; as shown in the Results) match the results of Punyasena *et al.* (2008) who showed that their abundance and richness decrease in areas with marked drought

### **The distinctiveness of the chaco woodlands**

Previous authors have excluded the chaco woodlands from the SDTF biome, citing floristic and environmental differences, including the factor that SDTF occurs only in frost-free areas, (Prado 1993a,b; Pennington *et al.*, 2000; Werneck *et al.*, 2011). However, we found that the sites we analysed in the Chaco Domain are compositionally

similar to other southern SDTFs (Fig 3a; additionally, some Chaco Domain sites clustered with sites from the Cerrado Domain and vice-versa in Fig. 2). In fact, the chaco woodlands from our dataset share 82% of their species with at least one of the SDTF nuclei of the Dry Diagonal. These results combined with the finding that many sites considered as SDTF experience significant frost (e.g. in the Piedmont and Misiones Nuclei) suggests that the chaco woodland may not be as abruptly distinct from SDTF as previously supposed, and that it may represent one extreme of a floristic gradient driven primarily by temperature. In support of the idea of Chaco as one end of an SDTF temperature gradient, a previous study (Sarkinen *et al.* 2011) found that 8.4% of SDTF specialist species occur in the Chaco Domain. However, further analyses including more sites from across the Chaco Domain and surrounding areas are needed to address its distinctness vs. similarity from neotropical SDTFs, and in particular, analyses which focus on the potentially distinct edaphic conditions often present in the Chaco (i.e. hypersaline soils) (Prado, 1993a).

Regarding the northern group, Santos *et al.* (2012) classified the arboreal caatinga (sites that occur along the border with Cerrado Domain) as part of the Caatinga SDTF Nucleus. However, performing the hierarchical clustering with a larger database we found that the arboreal caatinga is more similar to SDTFs found in the Cerrado Domain (support value  $\geq 0.9$  in Fig. 2), which could be related to higher edaphic similarities between arboreal caatinga and Cerrado Domain (calcareous, rich soils). The soil fertility (V%), for instance, of the arboreal caatinga and Cerrado Domain SDTFs from our database is  $57 \pm 2$  (mean  $\pm$  standard deviation) and  $46 \pm 13$ , respectively, whereas core caatinga vegetation has poorer soils (V% =  $35 \pm 14$ ). This result suggests that the identity of the arboreal caatinga should be revisited for conservation purposes,

since each Phylogeographic Domain (e.g. Caatinga, Cerrado, Amazonia, Atlantic rainforest) has a distinct environmental law in Brazil.

### **Unexplained variation**

While the environmental correlates of species composition in SDTF are fairly clear and straightforward to interpret, we have still failed to explain a large fraction (66.8%) of the variation in composition. There are many factors potentially important to determining the species composition of communities that we have not adequately accounted for, such as: 1) ecological drift (c.f. Hubbell, 2001) driving stochastic rearrangements of species distribution ranges through time; 2) biotic processes that were not measured (e.g. competition, natural enemies); 3) false absences in the surveys (e.g. researcher error, misidentification of species); 4) unmeasured descriptors of habitat quality (e.g. succession stage, degree of land degradation); 5) unsaturation, i.e. when species do not occupy all patches of suitable habitat (Titeux *et al.*, 2004); 6) other spatially and nonspatially structured environmental factors that were not measured. Moreover, a high proportion of unaccounted variation, ranging from about 33% to 75% (see Titeux *et al.*, 2004; Legendre *et al.*, 2009; Xiu *et al.*, 2012; Oliveira-Filho *et al.*, 2013), is actually a usual outcome in biogeography, since statistical noise in analyses with species presence/absence data is very often (ter Braak, 1986; ter Braak & Smilauer, 1998; Guisan *et al.*, 1999; Titeux *et al.*, 2004).

### **Concluding remarks**

The present study represents a new contribution to understanding patterns of community assembly of South American SDTFs. We showed that environmental conditions are significant factors underlying the floristic variation among SDTF patches spanning the Dry Diagonal that stretches from northeastern Brazil to Paraguay and northern Argentina. Thus, fragmentation and isolation of SDTFs as a consequence of glacial

cycles and older historical events, should not be assumed as the only drivers of species composition turnover in SDTFs.

Furthermore, these findings highlight the utility of the variance partitioning approach, which was an important tool to test the roles of historical versus environmental factors in driving patterns of species turnover across continental scales. Our demonstration that the floristic composition of SDTFs correlates strongly with climatic regime suggests that SDTF formations would have been affected by Pleistocene climatic changes (c.f. Prado & Gibbs 1993, Pennington *et al.*, 2000), assuming that species possessed the same climatic niches in the Pleistocene as at present. However, these climatic effects may have had more complex effects than producing a simple Pleistocene Arc of SDTF during the Last Glacial Maximum. Palaeoecological studies are beginning to reveal this complexity (Behling & Lichte, (1997; Burbridge *et al.*, 2004; Whitney *et al.*, 2011; 2013) and more such studies are needed. Paleodistribution modeling also holds promise for understanding the past distribution of SDTF (c.f. Werneck *et al.*, 2011), but given the high floristic variation of SDTFs documented here, SDTF clearly cannot be treated as a single unit (as in Werneck *et al.*, 2011). Rather, the distributions of floristically homogeneous subunits of SDTF and/or individual species should be modeled, both to understand the past distribution of SDTF and its future under global climate change.

Regarding the identity of SDTFs of the Dry Diagonal, our results showed that the chaco woodlands are not as floristically distinct from the SDTFs of the Dry Diagonal as has been assumed previously. Also, the second NMDS axis shows that the chaco woodlands and some southern SDTFs have floristic similarities with various sites of the northern group (i.e., Misiones Nucleus grouping with Cerrado Domain SDTFs and chaco woodlands grouping with Caatinga Nucleus in Fig. 3b). Therefore, we

suggest that the identity of the chaco woodlands and the exact circumscription of SDTFs merits further attention, since frost-affected nuclei such as Misiones and Piedmont would not fit all the definition criterias established by previous authors.

Finally, we call attention to the rapid loss of SDTFs due to mining, intensive agriculture and road building and the urgent need for conservation strategies. Most SDTF nuclei are poorly studied and lack sufficient floristic information to define conservation units. Our results showed that areas of the Dry Diagonal with distinct climate and soils have distinct floristic composition, but current conservation units do not cover all of the environmental heterogeneity present. For example, some SDTFs from the Mato Grosso do Sul state (central western Cerrado Domain) occur in saline soils (Decco *et al.*, 2010). However, the protected areas of this Brazilian state cover only savanna vegetation, and regions of SDTF are poorly studied, unprotected and endangered due to intensive cattle farming. Thus, we believe that using environmental data to define conservation units may greatly aid conservation prioritization until sufficient floristic information becomes available.

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## BIOSKETCH

**Danilo M. Neves** is a Brazilian Research Fellow at the University of Leeds. He is interested in ecology and evolutionary biology of plants, with an emphasis on niche evolution of Neotropical trees.

Author contributions: D.M.N., K.G.D and A.O.F. designed the paper; D.M.N., A.O.F. and M.L.B. assembled the database; D.M.N and K.G.D. analysed the data; A.O.F., M.L.B. and S.M.S. commented on earlier versions of the manuscript; and D.M.N., K.G.D. and R.T.P. led the writing.

**Table 1** Selected environmental variables ranked by the value of explanation in species composition variation across the South American Dry Diagonal. Adj.  $R^2$  Cum. = cumulative adjusted  $R^2$  of the forward selection; Axis1 =  $r$  (correlation coefficient) of the *post-hoc* correlations between the first NMDS axis and the environmental variables; Axis2 =  $r$  of the *post-hoc* correlations between the second NMDS axis and the environmental variables;  $R^2$  NMDS = global  $R^2$  of the *post-hoc* regressions between the first two NMDS axes and the environmental variables;  $P < 0.05$  in all cases, except for *post-hoc*  $R^2$  of the slope variable.

Variables	Adj. $R^2$ Cum.	NMDS1	NMDS2	$R^2_{ENVFIT}$
Actual evapotranspiration	0.06	-0.58	0.82	0.74
Temperature seasonality	0.11	-0.81	-0.58	0.72
Precipitation of driest month	0.14	-0.95	0.31	0.39
Sediment coarseness	0.16	0.99	-0.11	0.31
Min temperature of coldest month	0.18	0.99	0.12	0.49
Max water soil storage capacity	0.19	-0.38	0.93	0.56
Severity of water deficit	0.20	0.97	-0.22	0.52
Mean temperature of coldest quarter	0.21	0.89	0.46	0.43
Annual mean temperature	0.22	0.96	0.28	0.21
Soil fertility	0.22	-0.90	0.44	0.17
Length of water deficit	0.23	0.82	-0.58	0.58
Days of frost	0.23	-0.97	-0.25	0.19
Precipitation seasonality	0.24	0.99	-0.04	0.32
Altitude	0.24	0.47	0.88	0.05
Surface rockiness	0.25	0.86	0.50	0.03
Temperature annual range	0.25	-0.98	-0.19	0.57
Isothermality	0.25	0.91	0.42	0.68
Temperature daily range	0.25	-0.88	0.48	0.21
Min water soil storage capacity	0.26	-0.92	0.40	0.52
Potential evapotranspiration	0.26	0.53	0.85	0.08
Mean soil water storage capacity	0.26	-0.64	0.77	0.66
Precipitation of coldest quarter	0.26	-0.58	0.82	0.08
Mean temperature of driest quarter	0.26	0.96	0.28	0.48
Cloud cover	0.27	0.79	0.62	0.45
Aridity index	0.27	-0.62	0.78	0.71
Annual precipitation	0.27	-0.57	0.82	0.73
Precipitation of wettest month	0.27	-0.23	0.97	0.47
Precipitation of warmest quarter	0.27	-0.88	0.48	0.49
Mean temperature of warmest quarter	0.27	-0.06	-0.99	0.04
Mean temperature of wettest quarter	0.28	0.11	-0.99	0.05
Slope	0.28	-0.37	0.93	0.01

## Figure Legends

**Figure 1** Circles denote the location of tree species surveys used in this study ( $n = 282$ ). We note the major Phytogeographic Domains that form the South American Dry Diagonal in grey (Ca = Caatinga; Ce = Cerrado; Ch = Chaco; Cq = Chiquitanos) while moist domains are noted in white (At = Atlantic rain forest). SDTF nuclei are delimited by dashed lines (1 = Misiones; 2 = Piedmont); the Caatinga Nucleus covers the same area as the Caatinga Domain (Prado & Gibbs, 1993).

**Figure 2** Hierarchical clustering of Dry Diagonal SDTFs and chaco woodlands based on their tree species composition. The dissimilarity measure and linkage method were Jaccard and group average, respectively. Black bullets at the base of clusters indicate approximately unbiased bootstrap values  $\geq 0.90$  (Suzuki & Shimodaira, 2011). The floristic nuclei are discriminated by different colors: dark blue = chaco woodlands; light blue = Piedmont; green = Misiones; orange = Caatinga; red = Cerrado SDTFs; gray = Chiquitanos.

**Figure 3** Geographic variations in SDTF characteristics across the South American Dry Diagonal. The northern group from the hierarchical clustering analysis is discriminated by triangles and the southern group by bullets (see Fig. 2 and text). Values are illustrated by the color of the symbols, and warmer colours indicate higher values. Numbers in the header for each panel indicate minimum and maximum values. a) scores from the first axis of the non-metric multidimensional scaling (NMDS) analysis of species community composition. Black dashed line delimit frost-free (northern SDTFs) and frost-affected (southern SDTF and chaco woodlands) areas; b) scores from the second NMDS axis; c) mean minimum temperature of the coldest month; d) precipitation of the wettest month; e) temperature annual range; and f) maximum soil water storage capacity.

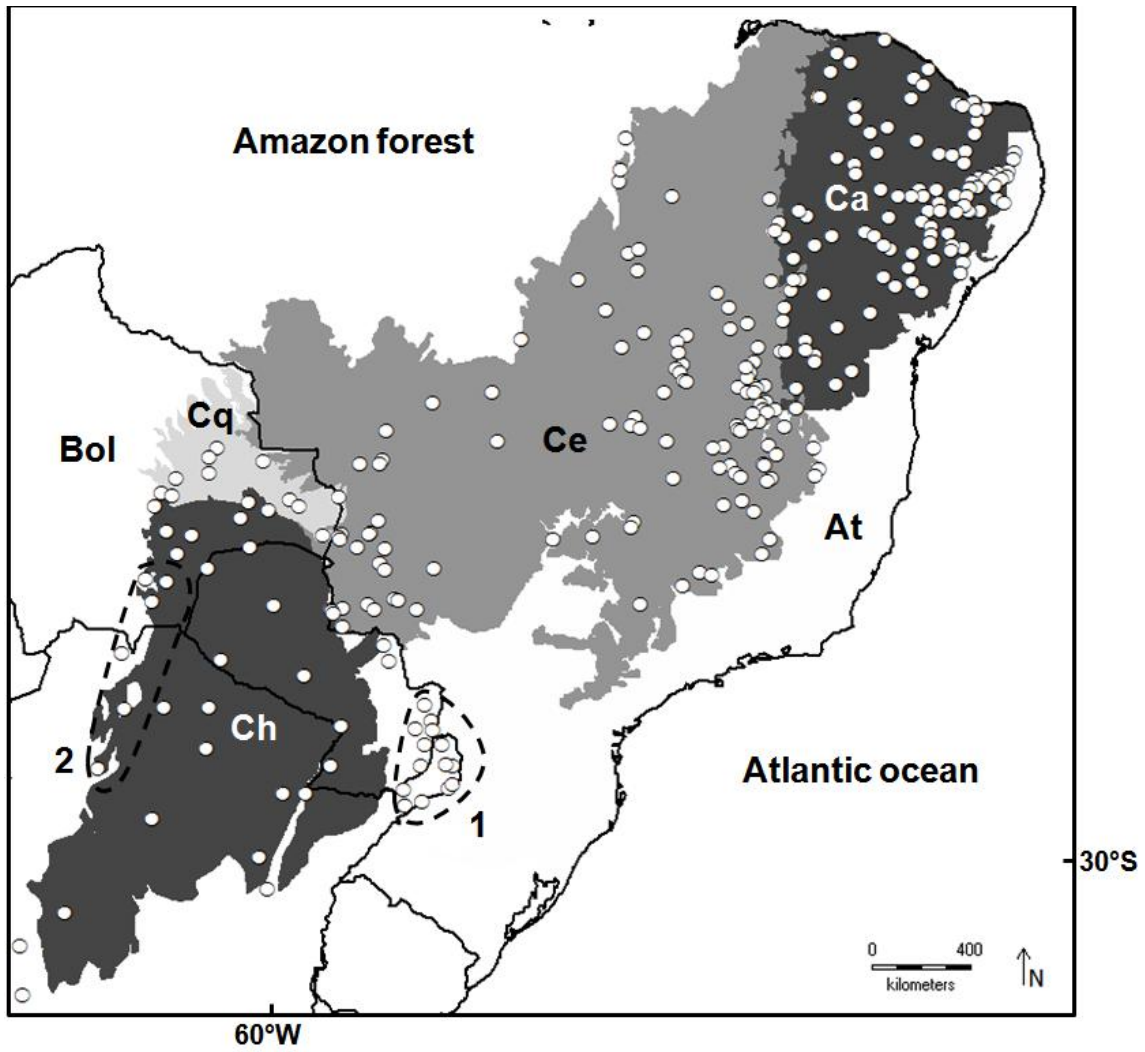


Figure 1

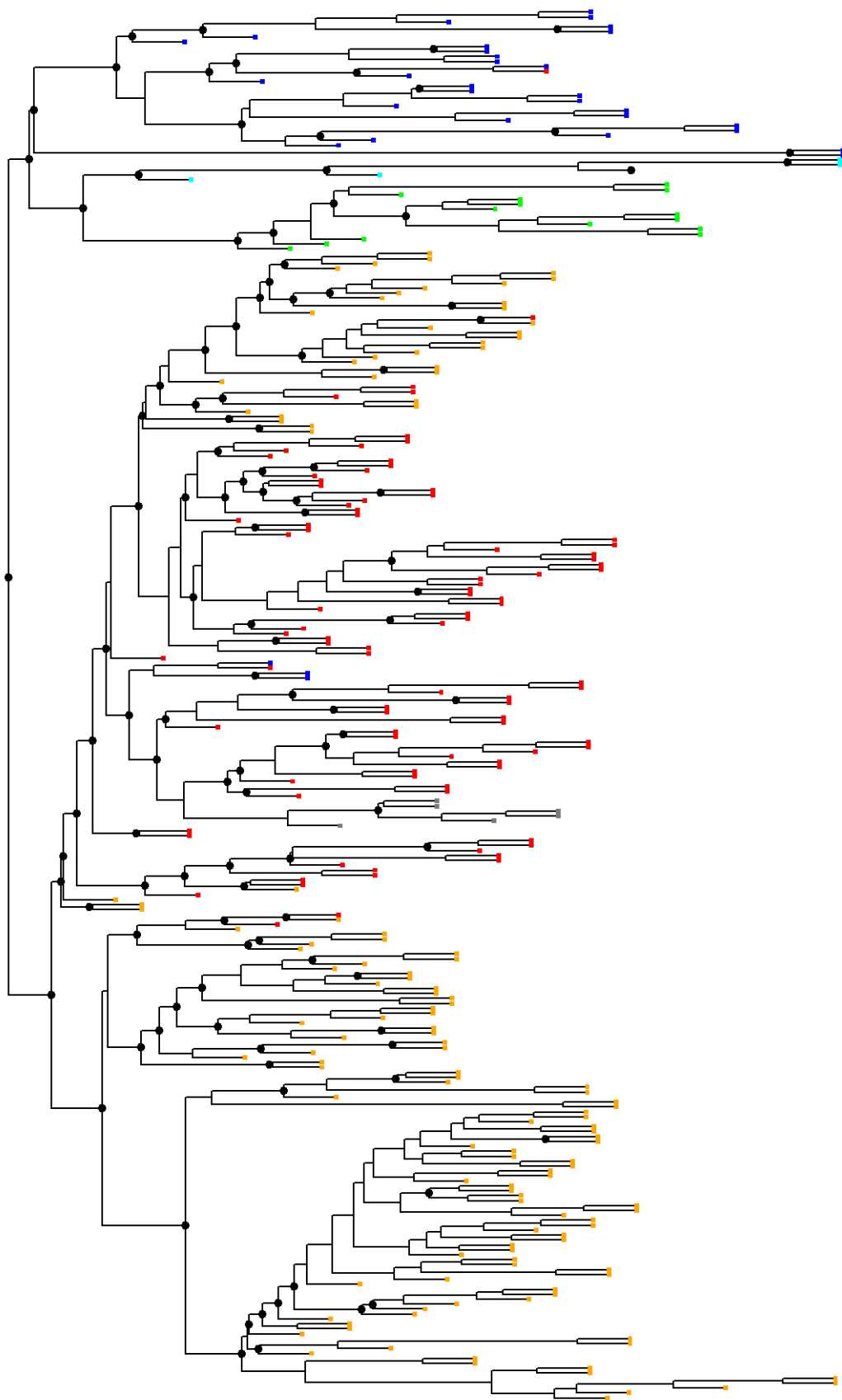
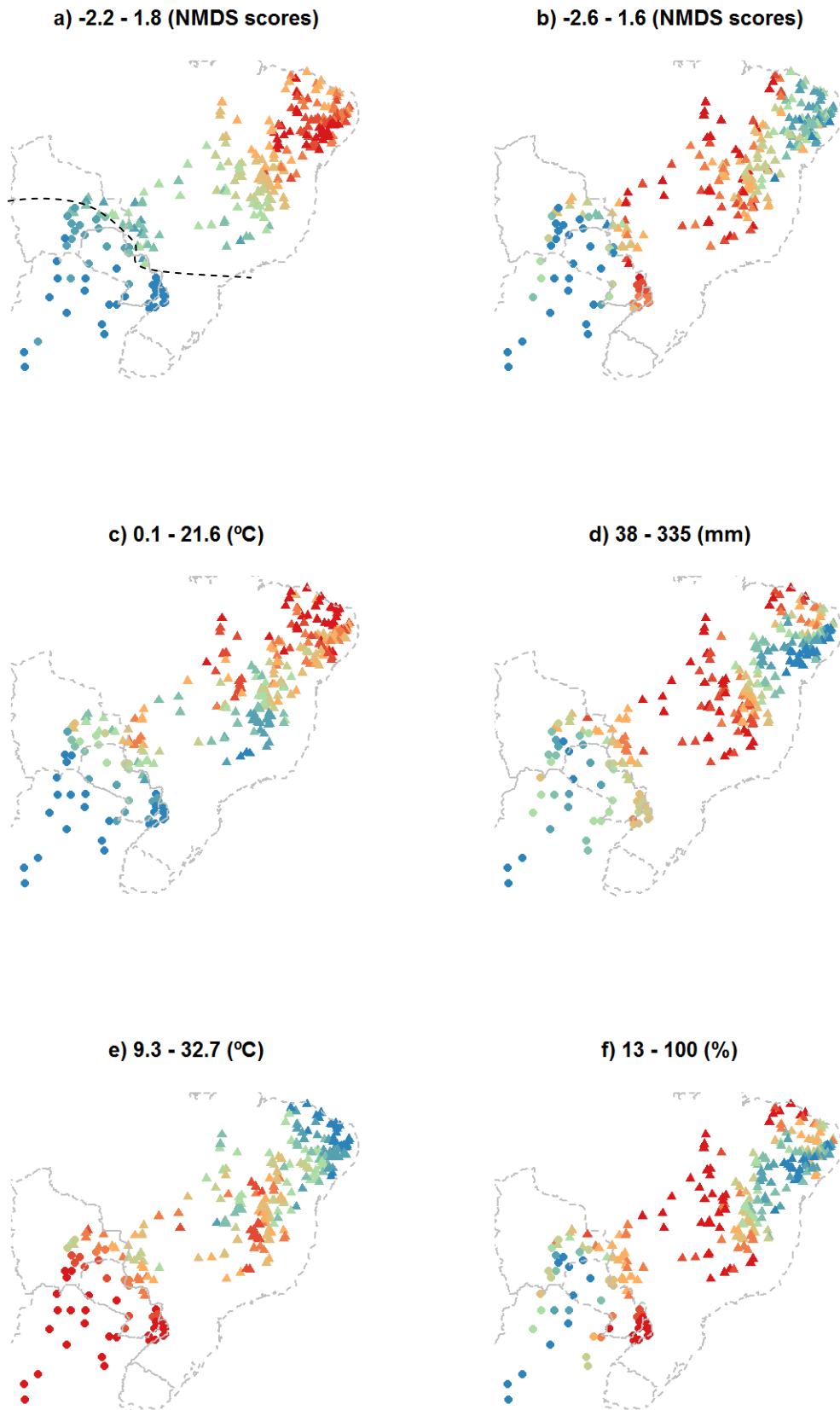


Figure 2



**Figure 3**

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**6. CAPÍTULO DOIS** - Spatial turnover of phylogenetic clades across the South American Dry Diagonal

Article type: Original article

# Spatial turnover of phylogenetic clades across the South American Dry Diagonal

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## ABSTRACT

**Aim** To investigate what drives the phylogenetic turnover across space in seasonally dry tropical forests (SDTFs) spanning ~4,300 km (north-south gradient) of the South American Dry Diagonal.

**Location** SDTFs extending from the Caatinga of northeastern Brazil to the Chaco of northern Argentina, an area referred to as the “Dry Diagonal”.

**Methods** The floristic inventories from our dataset were classified into two groups: the northern, comprised by 134 SDTF sites from the Caatinga, 91 SDTF enclaves scattered throughout the Cerrado Domain and 6 from the Bolivian Chiquitanos; and the southern, comprised by 14 SDTFs from the Misiones Nucleus, 5 from the Piedmont Nucleus, and 32 chaco woodland sites from the Chaco Domain. In order to assess the explanatory power of environmental factors, we subjected 36 environmental variables to a principal components analysis (PCA), and calculated an environmental dissimilarity matrix as the Euclidean distance in the space spanned by the PCA axes. We then used linear regression models to test the relation between phylobetadiversity and geographic distance, and compared the results to the relation between phylobetadiversity and environmental dissimilarities.

**Results** The linear models showed that phylobetadiversity is positively related to both geographic distance and environmental dissimilarity, and higher in the southern group. The environmental distance model revealed that environmental variation affects more strongly the southern group, which was congruent with a higher environmental heterogeneity in the southern region. The environmental gradients in the northern group were more homogeneous, and the environmental variation caused little effect on this group.

**Main conclusions** Because of the strong link between phylobetadiversity and environmental heterogeneity, and considering the threatened status of clades from the SDTF nuclei of the Dry Diagonal and the chaco woodlands, we believe that conservation planning should take temporal scales into account. Furthermore, if each SDTF nuclei of the Dry Diagonal and the chaco woodlands encompass disparate climatic conditions, conservation strategies should consider a spatial scale smaller than the one addressed on this paper. We highlight the importance of studies that attempt to understand the effect of climatic fluctuations on shaping the biodiversity through time, especially in a possible climate change scenario.

## Keywords

**Mean nearest taxon distance, niche conservatism, South American Dry Diagonal, South American diagonal of open formations**

## INTRODUCTION

The marked increase in phylogenetic studies now permits community structure to be assessed in an evolutionary perspective (Webb *et al.*, 2002), and the use of phylogenetic beta diversity approaches (hereafter “phylobetadiversity”) have been an important tool for conservation (Anacker & Harrison, 2012). The essential idea of phylobetadiversity is to measure how phylogenetic relatedness changes across environmental and spatial gradients (Graham & Fine, 2008). Along environmental gradients, for instance, the turnover of entire clades indicates that phylogenetic niche conservatism contributed to the observed patterns in community assembly (Graham & Fine, 2008; Anacker & Harrison, 2012).

If we are to pin point conservation strategies that consider scenarios of global climatic change, the phylobetadiversity approach may distinguish different evolutionary patterns within a given metacommunity, and thus the results could be used in conservation policies that take into account the phylogenetic diversity. In recent years, scientists have drawn attention to the high degree of phylogenetic geographic structure in the patchy seasonally dry tropical forests (SDTFs) in comparison to those of clades confined to rain forests (Richardson *et al.*, 2001; Gustafsson & Bittrich, 2003; Lavin, 2006; Erkens *et al.*, 2007; Sarkinen *et al.*, 2007; Torke & Schaal, 2008; Tripp, 2008; Kursar *et al.*, 2009; Pennington *et al.*, 2009). This higher tendency for sister species to occupy the same SDTF patch has been strongly supported by the phylogenetic structure found in robinoid legumes (Pennington *et al.*, 2009) as well as in clades of Indigofereae (Schrire, 2009). However, the probability of finding this same pattern for other SDTF lineages or for the whole SDTF metacommunity has not been tested.

In order to assess the patterns of phylogenetic structure in a given metacommunity (Webb *et al.*, 2002), a database that encompass community inventories,

with sites separated by a variety of geographic distances, and effective environmental information for each site is needed. Studies with the Neotropical palm family (Arecaceae) (Eiserhardt *et al.*, 2013), for instance, showed a remarkable continental-scale clade turnover, which was driven by a combination of limited niche evolution, with respect to temperature and soil tolerances, and limited dispersal. A similar database has been recently assembled for SDTF trees of the “Dry Diagonal” in eastern South America (see “Methods” below), but such a community phylogenetics approach for SDTFs remains unstudied.

With the purpose of providing information regarding the evolutionary history of SDTFs, here we performed some phylogenetic structure analyses at almost biome scale (spanning ~4,300 km in South America) to address the following hypotheses: *i.* The pattern of phylogenetic geographic structure shown by legume clades confined to SDTFs is also found for the whole SDTF metacommunity of the South American Dry Diagonal. *ii.* The spatial turnover of phylogenetic clades across the scattered SDTFs of the Dry Diagonal is related to both (a) isolation by distance patterns and (b) niche conservatism.

## **METHODS**

### **Study area**

The Dry Diagonal stretches from NE Brazil to Argentina, Paraguay and Bolivia, and occurs primarily in three Phytogeographic Domains which are named after the main vegetation types that occur within them (IBGE, 1993): Caatinga (tropical semi-arid thorn-woodlands), Cerrado (seasonal woody savannas) and Chaco (subtropical/tropical semi-arid thorn-woodlands) (Fig. 1). Prado and Gibbs (1993) defined three major nuclei of SDTF in the Dry Diagonal: 1) the Caatinga Nucleus, which occurs in northeastern Brazil and is the largest Nucleus (essentially the same area as the Caatinga Domain); 2) the Misiones Nucleus, which extends from the lower course of the Paraguay and Paraná

rivers to the upper Uruguay River in Misiones, Argentina; and 3) The Piedmont Nucleus, which occurs along the eastern base of the Andes in north-eastern Argentina. Scattered patches of SDTFs also occur in the Bolivian Chiquitanos (Linares-Palomino *et al.* 2011) and throughout the Cerrado Domain (Ratter *et al.*, 1988; Pennington *et al.*, 2000) on areas of fertile soils.

One environmental element in the definition of SDTFs is that they are a frost-free vegetation (Prado, 1993a,b; Pennington *et al.*, 2000) and regular winter frost is one factor that differentiates the chaco woodlands, found in northern Argentina, western Paraguay, south-eastern Bolivia, and the extreme western edge of Mato Grosso do Sul state in Brazil, from SDTF. However, large areas delimited as SDTF in the schematic maps of previous studies (e.g. Piedmont and Misiones, Prado & Gibbs 1993; Oliveira Filho *et al.*, 2006; Pennington *et al.*, 2009) also receive significant frost (see chapter one). Thus, because the exact definition of SDTF, and whether or not it receives significant frost, merits further attention in the future, we chose to include the chaco woodlands in our analyses, since they fit some other criteria of SDTF established by the aforementioned authors, such as seasonality of rainfall and deciduousness.

### **The database of SDTFs**

We extracted floristic inventory data from the TreeAtlas database ver. 2.0. This database consists of >2,000 geo-referenced localities for which lists of tree species (trees defined here as woody plants >3 m in height) were compiled from an extensive survey of published and unpublished (e.g. PhD theses) literature. A TreeAtlas site is defined by a single vegetation type contained in a circular area with a 10-km diameter. Therefore, where two or more vegetation types co-occur in one 10km area, there may be two geographically overlapping sites in the TreeAtlas database, each for a distinct vegetation type. The data derive primarily from inventories of woody vegetation (i.e.



plots, transects, and vegetation surveys). Surveys of specimens at major herbaria (e.g. K, NY, E, RB, BHC, UEC, SP) are then used to augment the lists for each location with any tree species that were collected within the 10-km diameter of the original TreeAtlas site, and within the same vegetation type. TreeAtlas does not include occurrence records without indication or evidence of vegetation type, and sites with clearly incomplete species lists. The latter is an important sieve because different sample efforts across sites may bias their descriptive power.

In order to better address the assumption of environment being a significant factor in driving phylobetadiversity, our floristic inventories were previously categorized into two environmentally distinct groups: the northern, comprised by 134 SDTF sites from the Caatinga, 91 SDTF enclaves scattered throughout the Cerrado Domain and 6 from the Bolivian Chiquitanos; and the southern, comprised by 14 SDTFs from the Misiones Nucleus, 5 from the Piedmont Nucleus, and 32 chaco woodland sites from the Chaco Domain (see Figure 1). The northern group climate ranges from semi-arid (long-lasting droughts) to seasonal (warm-rainy and mild-dry seasons), with low temperature seasonality, whereas the southern group is affected by tropical and temperate climates, which causes regular frosts during the dry winters and temperature maxima higher than 45° C during the rainy summer (Prado, 1993a,b; Pennington *et al.*, 2000).

### **Environmental distance metric**

The TreeAtlas database also includes altitudinal and environmental data for all sites, derived from multiple sources. Eight variables are related to edaphic substrate: mean, minimum and maximum monthly soil moisture (%), obtained from the International Soil Moisture Network ([www.ipf.tuwien.ac.at/insitu/](http://www.ipf.tuwien.ac.at/insitu/)); prevailing slope and aspect, obtained from CGIAR-CSI (2006); soil fertility (% base saturation, hereafter “V%”), soil

coarseness (% sand) and substrate rockiness (% surface of rock outcrops), extracted from a detailed map of soil types produced by EMBRAPA & IBGE (2003) using the RadamBrasil Soil Survey of the 1970s and 1980s, and additional field studies carried out by both governmental agencies (EMBRAPA & IBGE, 2003). Climatic variables include the mean duration (days) and severity (mm) of water-deficit periods, both extracted from Walter diagrams (Walter, 1985); the 19 bioclimatic variables produced by WorldClim 1.4, a high-resolution (1 km) database of global climate layers created by Hijmans *et al.* (2005); mean frequency of frosts (days), cloud cover (%) and cloud interception (mm), obtained from gridded datasets produced by Jones & Harris (2008); and three additional variables derived from WorldClim by Zomer *et al.* (2007, 2008): potential and actual evapotranspiration (mm) and an aridity index. A full description with details of protocols for TreeAtlas 2.0 can be found at <http://www.icb.ufmg.br/treetlan>.

In order to scrutinize the explanatory power of this environmental dataset, we subjected all the environmental variables to a principal components analysis (PCA) and omitted all components with standard deviations < 10% of the standard deviation of the first component. Environmental dissimilarity was then calculated as the Euclidean distance in the space spanned by the PCA axes (adapted from Eiserhardt *et al.*, 2013).

### **Phylogenetic dissimilarity and linear models**

First, we generated the phylogenetic community dissimilarity (PCD) using the *picante* 1.20 package (Kembel *et al.*, 2010) in the R Statistical Environment (R Development Core Team, 2012). A main advantage of this metric is that PCD can be partitioned into two components, a nonphylogenetic component that reflects shared species between communities and a phylogenetic component that reflects the evolutionary relationships among nonshared species (Ives & Helmus, 2010). Afterwards, we separated the

phylogenetic component of the PCD to yield the phylogenetic distance matrix for all pairwise comparisons using the 282 sample sites by 1765 species matrix and the community phylogeny of 1765 species. We then used ordinary least squares linear regression models to test the relation between phylobetadiversity and geographic distance (latitude and longitude), and compared the results to the relation between phylobetadiversity and environmental dissimilarities.

The community phylogeny was generated with the program Phylomatic (Webb & Donoghue, 2005) as implemented in the program Phylocom v 4.1 (Webb *et al.*, 2008) and using the angiosperm backbone tree (R20100701; <http://svn.phylodiversity.net/tot/megatrees/>). The taxonomic list submitted to Phylomatic followed the Angiosperm Phylogeny Group III classification (Angiosperm Phylogeny Group, 2009). Branch lengths in the community phylogeny were scaled to millions of years (Ma) using the branch-length-adjustment (bladj) option in Phylocom.

## RESULTS

The 51 southern sites sites harboured 832 species whereas the 231 northern sites included 1401 of the 1765 total arborescent species sampled. These findings reveal how floristically diverse the SDTFs are within the northern group (Fig. 1; Caatinga nuclei, Cerrado Domain SDTFs and the Bolivian Chiquitanos). From the perspective of community composition, the northern and southern vegetations are floristically distinct at the family, genus, and species level. The families Burseraceae and Nyctaginaceae show great biodiversity imbalance across the northern and southern groups, for example. Arborescent Burseraceae (e.g., *Commiphora leptophloeus*) are found in many northern sites and very few southern sites, and vice versa for the Nyctaginaceae (e.g., *Pisonia*). *Commiphora leptophloeus* (Mart.) J.B.Gillett was found in 123 of the 231

northern sites (~53%) and only in one of the 51 southern sites (~1%), for example. In contrast, *Pisonia zapallo* Griseb. occurred in 33 of the 51 southern sites (~65%) yet was sampled in just 16 of the 231 northern sites (~7%). Such floristic differences commonly found at taxonomic levels above the species are reflected in the results of the community phylogenetic analysis.

The 1765 tree species of the the Phylomatic-generated community phylogeny range from tree ferns (the earliest branching lineage) to mostly eudicot species including arborescent Cactaceae and Euphorbiaceae species (Fig. 1). The family Fabaceae (Leguminosae) is by far the most species rich woody family. The subfamilies of Fabaceae, Caesalpinioideae, Mimosoideae (the clade marked by “mim”), and Papilionoideae (the clade marked by “pap”) are each more species rich than any other plant family sampled during this study.

The linear models showed that phylobetadiversity is positively related to both geographic distance (adjusted  $R^2_{north} = 0.14$ ,  $P < 0.001$ , green line in Fig. 3; adjusted  $R^2_{south} = 0.19$ ,  $P < 0.001$ , red line in Fig. 3) and environmental dissimilarity (adjusted  $R^2_{north} = 0.13$ ,  $P < 0.001$ , green line in Fig. 5; adjusted  $R^2_{south} = 0.31$ ;  $P < 0.001$ ; red line in Fig. 5), and higher in the southern group. The environmental distance model revealed that environmental variation affects more strongly the southern group, which was congruent with a higher environmental heterogeneity in the southern region (black triangles covering more space in both first and second axes in Fig. 4). The environmental gradients in the northern group were more homogeneous, and the environmental variation caused little effect on this group.

## DISCUSSION

Our results appear to support a niche-based control of phylobetadiversity in SDTF tree communities of the Dry Diagonal (niche conservatism). The higher phylogenetic turnover in southern SDTFs and chaco woodlands being congruent with a higher environmental heterogeneity in the southern region suggests that ecological determinants are the main factor driving phylobetadiversity in SDTFs. This result reflect that northern clades are more widespread, whereas southern ones are small ranged, probably because the southern region encompass such disparate environmental conditions that whole clades might have evolved traits that preclude them of being widespread (Graham & Fine, 2008).

Overall, the most realistic picture is a spatial-niche system controlling the phylobetadiversity with different strengths. Many authors have showed evidences of phylogenetic niche conservatism in Neotropical SDTFs (Lavin *et al.*, 2000; 2003; 2004; Becerra, 2003; 2005; Pennington *et al.*, 2004; 2009; Edwards *et al.*, 2005; Lavin, 2006; Becerra & Venable, 2008; Donoghue, 2008; Tripp, 2008; Pirie *et al.*, 2009; Schrire *et al.*, 2009), and one of the main conclusions emerged from these studies is that sister species often occupy the same nucleus of SDTF, indicating a high degree of phylogenetic geographic structure (Pennington *et al.*, 2009). Our results support this niche-based control, and there is higher phylogenetic turnover (phylobetadiversity) where the environmental variation is higher (Fig. 5), i.e. sorting among entire clades between communities is more likely if environmental turnover is more abrupt (e.g., southern SDTFs and chaco woodlands).

Considering this strong link between the phylobetadiversity in SDTFs and the environmental heterogeneity, it seems that ecological factors are capable of shaping biodiversity over time, since the breadth of the suitable habitat for SDTFs may change

along with climatic fluctuations. In other words, the continuous ecological processes may be the main factors driving the patterns of biodiversity in the Dry Diagonal, and therefore we believe that the southern group has assembled under different levels of temperature and drought regimes compared to the northern group, which suggests distinct evolutionary histories.

A recent paleomodelling article assessed the environmental suitability for SDTFs of the Dry Diagonal under three models: Last Glacial Maximum (21 thousand years BP), Mid-Holocene (6 thousand years BP) and current climate. Werneck *et al.* (2011) results predicted stable areas for SDTF in the Caatinga and Cerrado Domains, as well as in the Bolivian Chiquitanos. In contrast, most of the southern group area (Misiones and Piedmont) was predicted as unsuitable for SDTF, which demonstrates different historical scenarios for the northern and southern groups, and thus supports our conviction that these groups might have experienced disparate evolutionary histories.

These are assumptions of considerable importance for conservation strategies, mainly because SDTFs are worldwide threatened (Miles *et al.*, 2006). Considering that their niche evolution are limited on evolutionary timescales (due to niche conservatism), species from both SDTF and chaco woodlands of the Dry Diagonal might fail to adapt in response to rapidly changing climates. Thus, we suggest that conservation units should be large enough to protect population sizes that might thrive in a climatic change scenario, especially in the southern group, since the niche breadth of southern clades are narrower when compared to northern SDTFs.

### **Concluding remarks**

Because of the strong link between phylobetadiversity and environmental heterogeneity, and considering the threatened status of clades from the SDTF nuclei of the Dry Diagonal and the chaco woodlands, we believe that conservation planning should take

temporal scales into account. Furthermore, if each SDTF nuclei of the Dry Diagonal (e.g., Caatinga, Cerrado Domain SDTFs, Misiones and Piedmont) and the chaco woodlands encompass disparate climatic conditions, conservation strategies should consider a spatial scale smaller than the one addressed on this paper (northern and southern groups). Although, more accurate studies, which means an assessment of the different nuclei and the chaco woodlands separately, are needed to test this assumption. To conclude, we emphasize the niche-based controls of phylobetadiversity in SDTFs of the Dry Diagonal and we also highlight the importance of studies that attempt to understand the effect of climatic fluctuations on shaping the biodiversity through time, especially in a possible climate change scenario.

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## **BIOSKETCH**

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Author contributions: D.M.N., K.G.D and A.O.F. designed the paper; D.M.N., A.O.F. and M.L.B. assembled the database; D.M.N and K.G.D. analysed the data; A.O.F., M.L.B. and S.M.S. commented on earlier versions of the manuscript; and D.M.N., K.G.D. and R.T.P. led the writing.

## LIST OF FIGURES

**Figure 1** Circles denote the location of tree species surveys used in this study ( $n = 282$ ). We note the major Phytogeographic Domains that form the South American Dry Diagonal in grey (Ca = Caatinga; Ce = Cerrado; Ch = Chaco; Cq = Chiquitanos) while moist domains are noted in white (At = Atlantic rain forest). SDTF nuclei are delimited by dashed lines (1 = Misiones; 2 = Piedmont); the Caatinga Nucleus covers the same area as the Caatinga Domain (Prado & Gibbs, 1993).

**Figure 2** The Phylomatic-generated community phylogeny of the 1765 tree species sampled from the 282 seasonally dry tropical forests of the South American open biomes. The labels of the terminal branches have been omitted in order to emphasize the distribution of branch lengths and identification of a few of the principal or species-rich subclades. Mim = Mimosoidae; pap = Papilionoideae; Ma = million years.

**Figure 3** A distance model detailing the phylogenetic beta diversity as a function of geographical distance (grey-shaded data points for within groups comparisons, black data points for between groups comparisons). Adjusted  $R^2_{north} = 0.14$ ,  $P < 0.001$ , green line; adjusted  $R^2_{south} = 0.19$ ,  $P < 0.001$ , red line. The blue line represents the slopes of the ordinary least squares linear model between phylogenetic turnover and geographic distance for all 282 SDTFs. Ma = million years.

**Figure 4** Principal Component Analysis (PCA) showing the environmental heterogeneity on 282 SDTFs of the South American Dry Diagonal. The northern group is discriminated by open circles and the southern group by triangles.

**Figure 5** A distance model detailing the phylogenetic beta diversity as a function of environmental distance (grey-shaded data points for within groups comparisons, black data points for between groups comparisons). Adjusted  $R^2_{north} = 0.13$ ,  $P < 0.001$ , green line; adjusted  $R^2_{south} = 0.31$ ,  $P < 0.001$ , red line. The blue line represents the slope of the ordinary least squares linear model between phylogenetic turnover and environmental distance for all 282 SDTFs. Ma = million years.

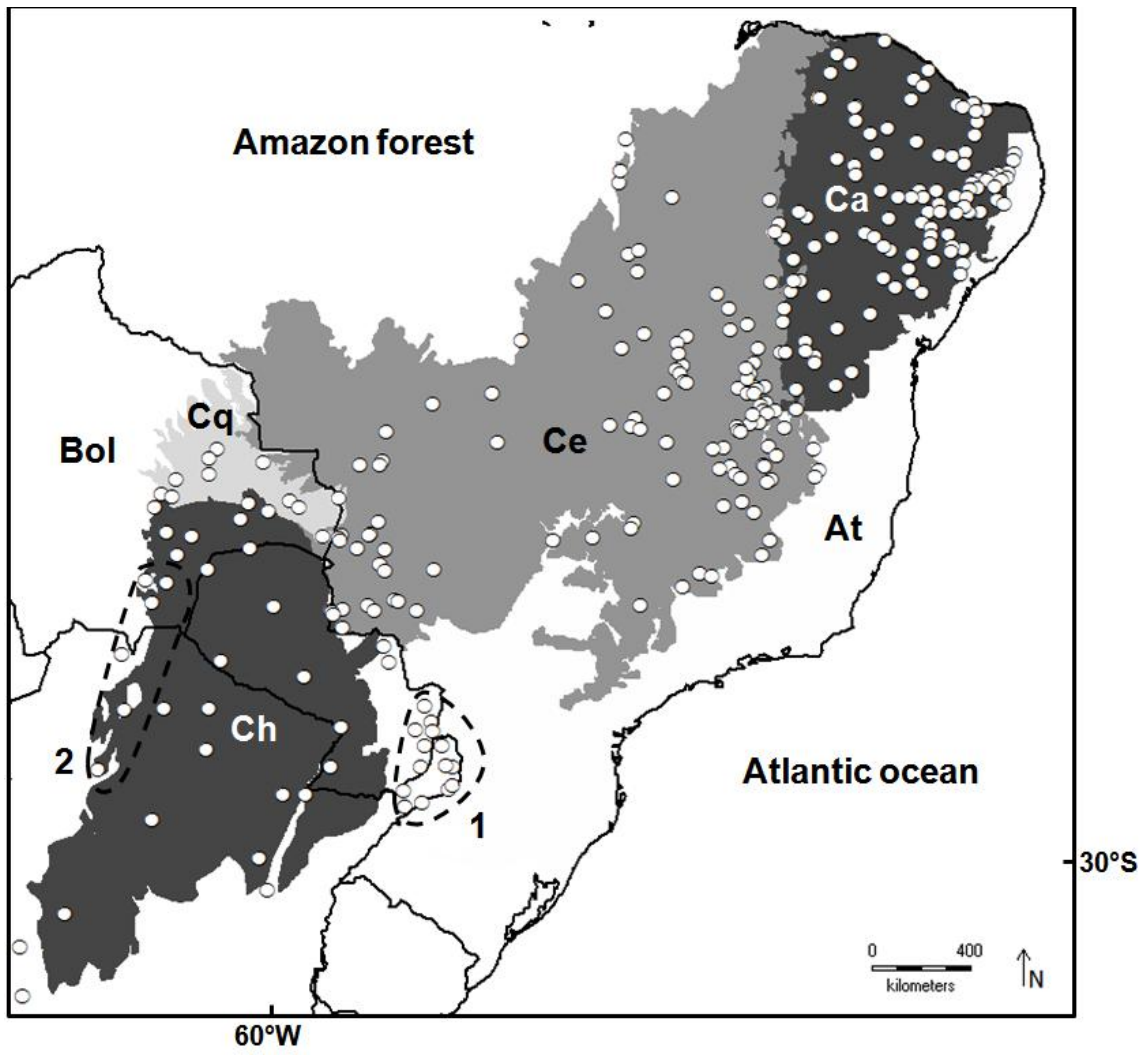


Figure 1

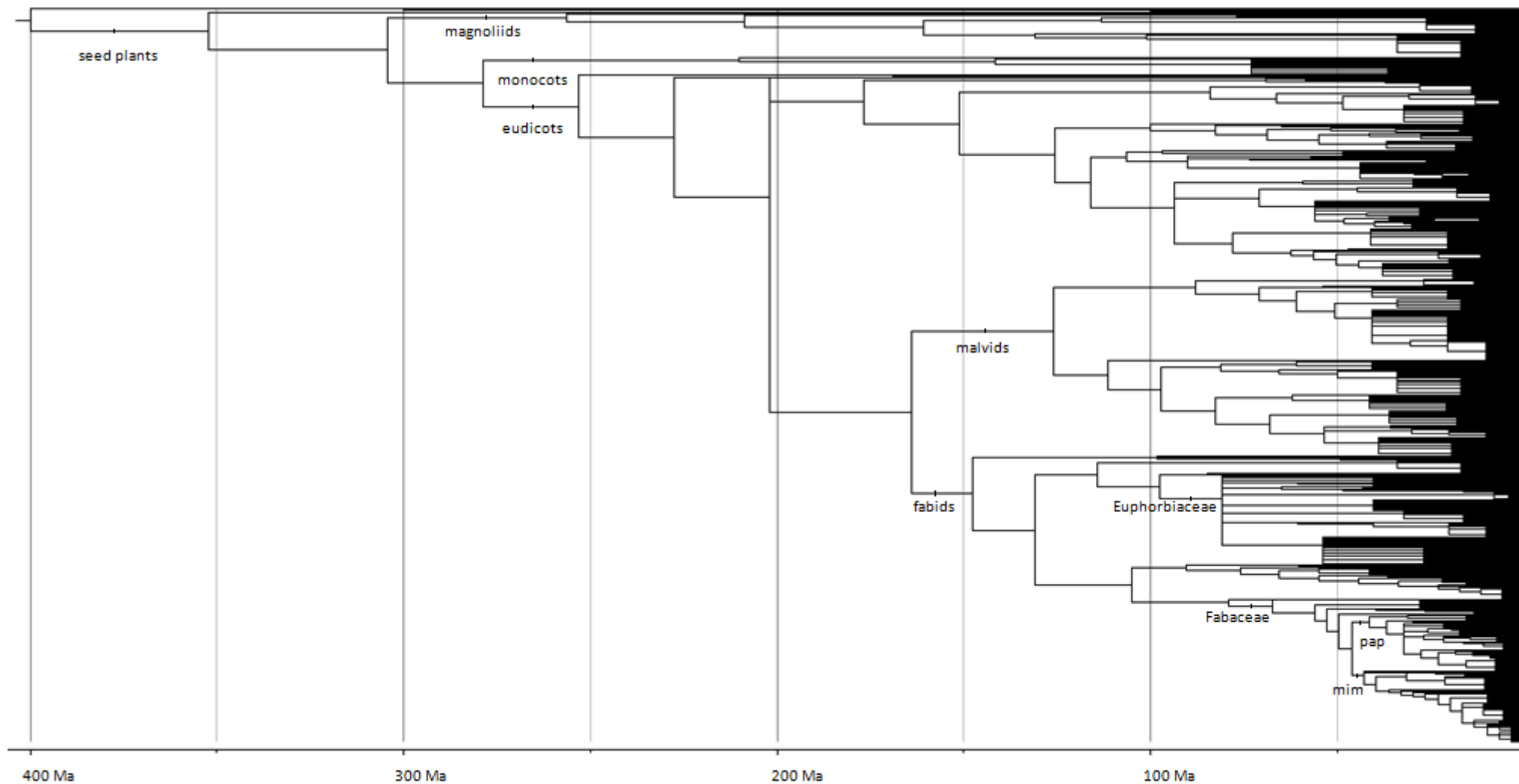
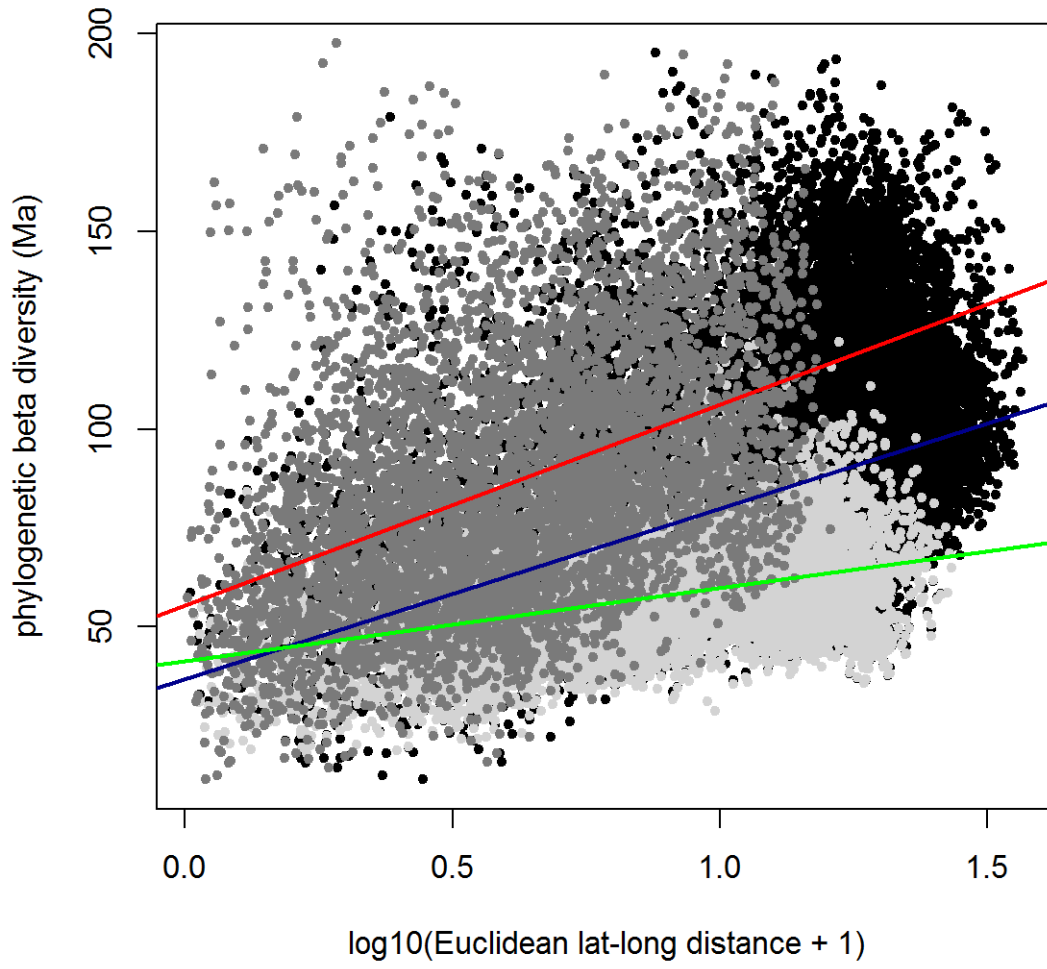
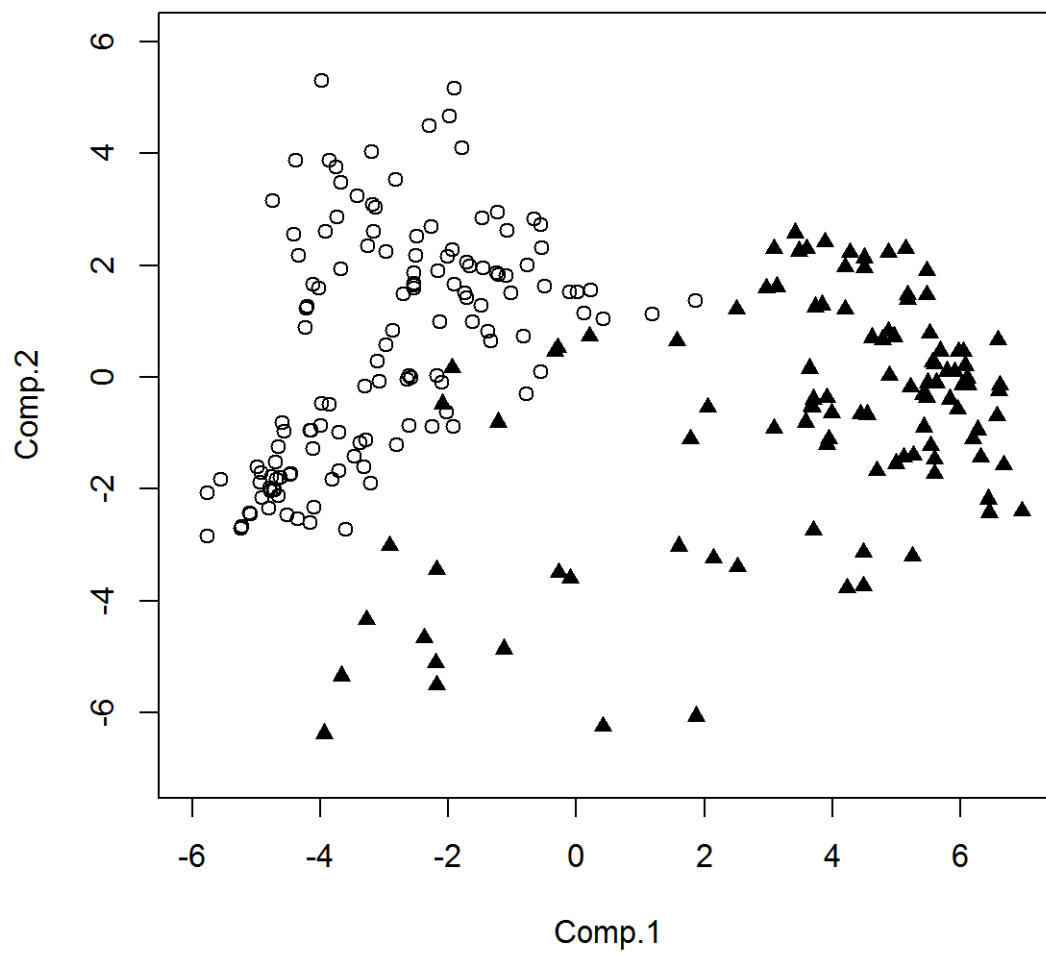


Figure 2

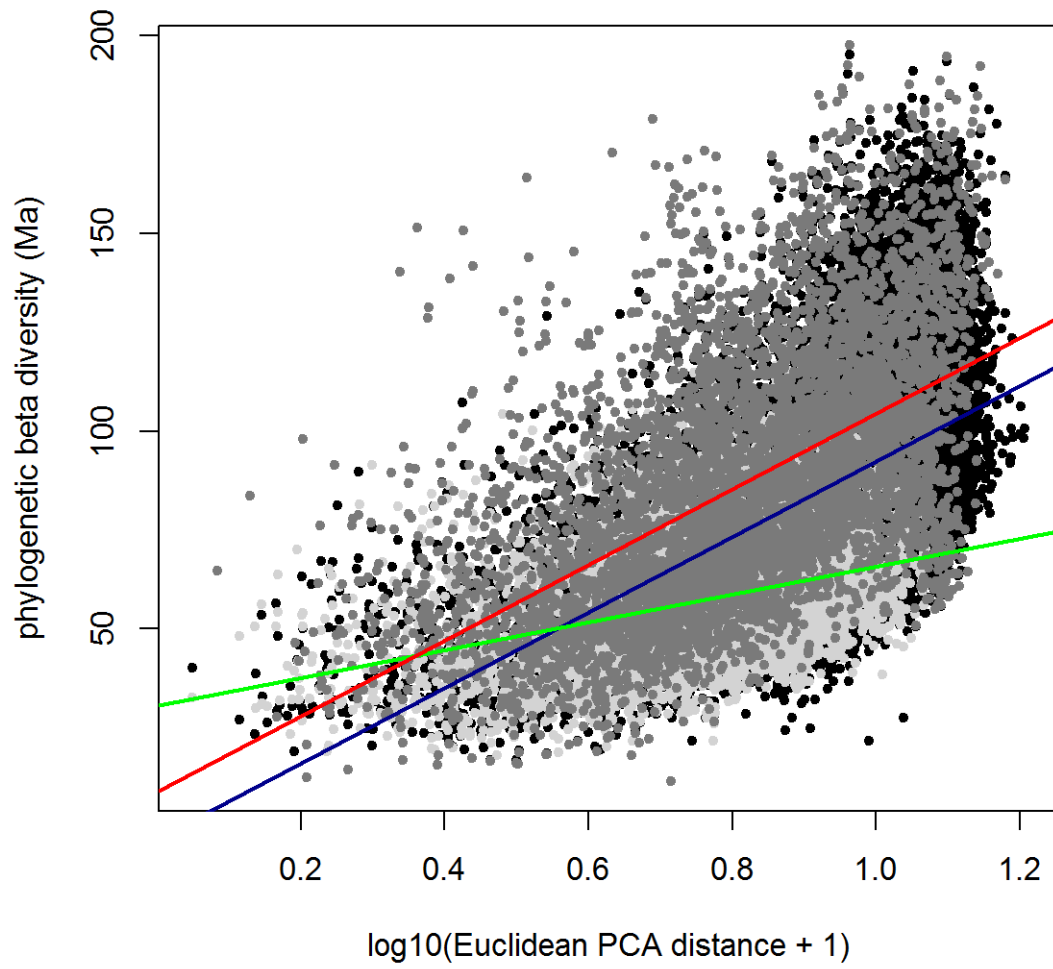


**Figure 3**



**Figure 4**





**Figure 5**

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## CONSIDERAÇÕES FINAIS

O presente trabalho representa uma importante contribuição para o entendimento dos padrões de variação florística e filodiversidade beta em florestas sazonalmente secas (FTSS) do diagonal sul-americano das formações abertas (diagonal seco). Nossos resultados sugerem que o cenário mais realista é um sistema clima-solo-distância afetando a distribuição de espécies (1º capítulo) e as relações filogenéticas (2º capítulo) em diferentes escalas espaciais e temporais, bem como diferentes intensidades. De um lado, a heterogeneidade ambiental parece ser o fator mais parsimonioso explicando ambos os padrões de *turnover* filogenético e variação florística entre FTSS, conforme corroboram os resultados encontrados para o grupo sul do 2º capítulo (Piedmont, Misiones e Chaco), ou seja, maior variação ambiental sendo congruente com maior filodiversidade beta. Por outro lado, a possível vicariância pleistocênica também pode ter influenciado esse padrões, porém, com intensidade menor, tendo em vista que a deriva ecológica em grandes metacomunidades dependendo apenas da dinâmica neutra pode permanecer insignificante por milhões de anos. Contudo, a principal conclusão que emerge deste trabalho é a congruência entre diversidade (beta e filodiversidade beta) e heterogeneidade ambiental, o que enfatiza a importância de estudos para a compreensão do efeito das flutuações climáticas em FTSS, devido principalmente ao alto grau de ameaça dessas formações e somado a um possível cenário de mudança climática global. Ressaltamos ainda que, para a proposição de unidades de conservação baseando-se na dissimilaridade entre as diferentes FTSS, na ausência de dados florísticos eficientes seria possível fazer uso informações edafo-climáticas, conforme abordado neste estudo.