Universidade Federal da Grande Dourados Faculdade de Ciências Exatas e Tecnologia

Traços Funcionais na Evolução e Estruturação de Florestas Estacionais Functional Traits in the Evolution and Structuring of Seasonal Forests

Larissa Oliveira Vilela

Dourados 2024

Larissa Oliveira Vilela Bióloga

Traços Funcionais na Evolução e Estruturação de Florestas Estacionais Functional Traits in the Evolution and Structuring of Seasonal Forests

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Tese apresentada para obtenção do título de Doutora em Ciência e Tecnologia Ambiental. Linha de pesquisa: Ciência Ambiental.

Dourados 2024

Dados Internacionais de Catalogação na Publicação (CIP).

V699t Vilela, Larissa Oliveira Traços Funcionais na Evolução e Estruturação de Florestas Estacionais [recurso eletrônico] / Larissa Oliveira Vilela. -- 2024. Arquivo em formato pdf.
Orientadora: Zefa Valdivina Pereira. Tese (Doutorado em Ciência e Tecnologia Ambiental)-Universidade Federal da Grande Dourados, 2024. Disponível no Repositório Institucional da UFGD em: https://portal.ufgd.edu.br/setor/biblioteca/repositorio
1. Sinal filogenético. 2. Restauração ecológica. 3. Interações ecológicas. 4. Manejo ambiental. 5. Resiliência ecológica. I. Pereira, Zefa Valdivina. II. Título.

Ficha catalográfica elaborada automaticamente de acordo com os dados fornecidos pelo(a) autor(a).

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# DEDICATÓRIA

À minha avó Maria Oliveira (*in memoriam*), à minha ancestralidade feminina: a minha reverência. Vos dedico essa tese e meus dias.

### **Nuestro Mundo**

Nuestro mundo divino mundo te amo tanto Con tus ríos y tus bosques me ilumino Con mis ojos puedo ver tu belleza Con tus plantas y animales maravillosos Tus montañas y tus aguas cristalinas

Pachamama, madre tierra, madre de todo Perdoname ya tus hijos que te hicieron daño Pachamama, madre tierra, madre de todo Curame ya tus hijos que te aman tanto

> Espíritu de la vida ayúdanos A curar y sanar el corazón Cada uno puedo vivir en la luz Vivir en paz y amor es el camino Vivir en paz y amor te lo pido

> > Pachamama...



## AGRADECIMENTOS

Agradeço profundamente à mamãe divina natureza, fonte de inspiração e sabedoria, que me ensinou a olhar o mundo com os olhos da alma e a sentir a conexão entre todos os seres. Graças à beleza das flores, à leveza dos pássaros e à resiliência das árvores, pude encontrar inspiração para escrever esta tese. Gratidão pela vida, pelo ar puro que respiro e pela terra que me sustenta. A perfeição da natureza que me mostrou a importância de amar, cuidar e preservar este planeta. Agradeço de todo coração a mãe natureza, por me ensinar que servir a todos os seres é a maior das missões.

Agradeço profundamente aos povos da floresta, sagrados guardiões, que com sua sabedoria ancestral têm preservado a harmonia entre o ser humano e a natureza, na coexistência pacífica com todas as formas de vida. Expresso aqui meu profundo respeito e gratidão por nos fazerem lembrar que todos somos parte de um mesmo e grandioso ciclo de vida.

Gostaria de expressar a minha sincera gratidão a todas as instituições públicas de ensino e a todos professores que tornaram possível a minha jornada acadêmica e me ajudaram a realizar os meus sonhos. Desde a escola até a universidade, pude contar com uma educação de qualidade e acessível, que me permitiu chegar até aqui. Em defesa daquilo que é público, pela valorização e democratização do acesso à ciência e à educação, e em busca de uma sociedade justa e igualitária, para que outros mais possam chegar tão longe quanto eu.

Agradeço a toda força, determinação e dedicação colocada por mim na minha jornada acadêmica, na realização dos meus sonhos. Agradeço ao sopro de vida que habita em mim, por toda coragem e perseverança, por mesmo sozinha nunca ter desistido ou desacreditado do meu próprio potencial. Agradeço por nunca ter perdido de vista meu amor pelo conhecimento, por ter mantido viva a chama da curiosidade e da descoberta e por fazer dos obstáculos uma oportunidade de crescimento e evolução.

Agradeço ao Instituto Universalista Flor das Águas do Rio Apa que tem me fortalecido e me motivado a continuar com todo o meu coração a minha jornada. Agradeço pela oportunidade de liderar essa missão sagrada, por poder ver e sentir a beleza da conexão humana em sua forma mais pura. Agradeço às sagradas medicinas da floresta, que me iluminam e me curam. Através delas, pude me manter firme, me conectar com a sabedoria ancestral da Terra, redescobrir meu propósito e sentir a presença divina em cada aspecto da vida. Minha gratidão é infinita por todos que fazem parte dessa irmandade.

Agradeço à minha mãe Ilza Oliveira Feitoza, por ser meu exemplo de força e coragem. Por ter me ensinado a importância da educação, da perseverança e da honestidade. Por me motivar a explorar o mundo e a buscar sempre o melhor de mim mesma. Seu amor incondicional, suas lições valiosas e seu apoio incansável moldaram a pessoa que sou hoje. Sou imensamente grata por tudo o que fez e continua fazendo por mim.

Agradeço à minha vózinha Maria Oliveira de Souza (*in memoriam*), por todo amor, por todo cuidado, por todo colo. Agradeço pelo primeiro contato com as letras, os números e as cores. Agradeço por estar sempre ao meu lado me guiando e me trazendo força. Tenho muito orgulho de ser neta de dona Maria e ser a primeira doutora da minha família. Honro e agradeço.

Agradeço ao meu companheiro e parceiro de vida Rodrigo Paredes por me encorajar a buscar meus sonhos, a enfrentar desafios e a acreditar em meu potencial. Agradeço por todo apoio, por toda paciência, por cada sorriso, cada colo, cada gesto de amor. Gratidão por tê-lo ao meu lado nessa jornada misteriosa chamada vida.

Por fim, desejo expressar minha mais profunda gratidão àqueles que caminharam ao meu lado nos momentos de dúvida e incerteza. Descobri que por trás de cada trabalho acadêmico reside também um ser humano que anseia por suporte. O conhecimento só se tece plenamente quando o indivíduo é acolhido por uma rede de apoio, encontrando conforto emocional no encorajamento daqueles que estão ao nosso lado. A cada um de vocês, que de alguma forma tocaram minha vida e contribuíram para esta conquista, meu sincero e profundo obrigada.

Agradeço.

## RESUMO

Traços funcionais são atributos morfológicos, fisiológicos e comportamentais que influenciam o desempenho das plantas em seu ambiente, crucial para seu estabelecimento, sobrevivência e reprodução ao longo do tempo evolutivo. Esta tese investiga os traços funcionais das plantas lenhosas nas Florestas Estacionais de Mato Grosso do Sul, Brasil, explorando sua evolução, distribuição e impacto no funcionamento dos ecossistemas. O primeiro capítulo foca na análise do sinal filogenético dos traços funcionais, investigando a conservação e superdispersão desses atributos em diferentes fitofisionomias das Florestas Estacionais. Utilizando estatística D para estimar o sinal filogenético e a Análise de Correspondência (CA) para explorar padrões nas associações entre as variáveis. Foram identificados padrões distintos de conservação filogenética. Traços como o tamanho da flor e a síndrome de dispersão foram identificados como conservados, enquanto características como espinescência e capacidade de rebrota mostraram-se mais aleatórias ou superdispersas. Estes padrões refletem adaptações específicas a pressões seletivas, incluindo distúrbios e interações mutualísticas ao longo da evolução das comunidades vegetais. O segundo capítulo agrupa espécies em clusters com base em seus traços funcionais, analisa a sobreposição e as relações entre esses grupos funcionais em um espaço multivariado e busca entender a distribuição espacial das espécies dentro desses clusters em relação a fatores ambientais, como clima, pedologia e geomorfologia. Este capítulo destaca a importância de traços reprodutivos e florais na diferenciação dos clusters e a adaptação flexível das espécies às condições ambientais variáveis, revelando preferências por determinados ambientes topográficos e climáticos dentro do Mato Grosso do Sul. Esta tese contribui significativamente para o entendimento teórico e aplicado dos traços funcionais como elementos fundamentais na estruturação e dinâmica das comunidades vegetais das Florestas Estacionais. Ademais, estabelece uma base sólida para futuras pesquisas e iniciativas de conservação e restauração ecológica em ecossistemas similares, em face às mudanças ambientais globais.

#### Palavras-chave

Sinal filogenético, Adaptabilidade ecológica, Interações ecológicas, Restauração ecológica, Manejo ambiental, Resiliência ecológica

#### ABSTRACT

Functional traits are morphological, physiological, and behavioral attributes that influence plant performance in their environment, crucial for their establishment, survival, and reproduction over evolutionary time. This thesis investigates the functional traits of woody plants in the Seasonal Forests of Mato Grosso do Sul, Brazil, exploring their evolution, distribution, and impact on ecosystem functioning. The first chapter focuses on the analysis of the phylogenetic signal of functional traits, investigating the conservation and superdispersion of these attributes in different phytophysiognomies of Seasonal Forests. Using D statistics to estimate the phylogenetic signal and Correspondence Analysis (CA) to explore patterns in the associations between variables, distinct patterns of phylogenetic conservation were identified. Traits such as flower size and dispersal syndrome were identified as conserved, while characteristics such as spinescence and resprouting capacity showed more randomness or superdispersion. These patterns reflect specific adaptations to selective pressures, including disturbances and mutualistic interactions throughout the evolution of plant communities. The second chapter groups species into clusters based on their functional traits, analyses the overlap and relationships among these functional groups in a multivariate space, and seeks to understand the spatial distribution of species within these clusters in relation to environmental factors such as climate, soil, and geomorphology. This chapter highlights the importance of reproductive and floral traits in differentiating clusters and the flexible adaptation of species to variable environmental conditions, revealing preferences for specific topographic and climatic environments within Mato Grosso do Sul. This thesis significantly contributes to the theoretical and applied understanding of functional traits as fundamental elements in the structure and dynamics of plant communities in Seasonal Forests. Furthermore, it establishes a solid foundation for future research and initiatives in conservation and ecological restoration in similar ecosystems, in the face of global environmental changes.

#### Keywords

Phylogenetic signal, Ecological adaptability, Ecological interactions, Ecological restoration, Environmental management, Ecological resilience

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## 1 Apresentação

Esta tese explora os traços funcionais de espécies arbustivas e arbóreas presentes em Florestas Estacionais. Nesta apresentação, são descritos conceitualmente os traços funcionais, destacando as interações e efeitos ecológicos que podem ser mediados por eles, além das vantagens e desafios das abordagens baseadas nesses traços. Também é abordado como o estudo de atributos funcionais pode contribuir para a compreensão da história evolutiva das plantas e da formação e manutenção de comunidades, além de fornecer subsídios para restauração ecológica em larga escala nos trópicos e preencher lacunas teóricas ainda existentes. Finalmente, são contextualizadas as abordagens funcionais em Florestas Estacionais e evidenciado como esta tese pode contribuir para esses avanços.

Quando analisamos o processo de evolução dos organismos ao longo da história da vida na Terra, observamos uma série de características adaptativas selecionadas ao longo de suas histórias evolutivas. Tais características, resultantes de um longo processo de seleção natural, conferiram aos organismos a capacidade de sobreviver, se reproduzir e obter recursos nesses ambientes. À medida que essas características passam a influenciar o crescimento, sobrevivência e reprodução do indivíduo, bem como a mediar suas interações com o ambiente, podemos considerá-las como atributos ou traços funcionais (Caruso et al., 2020).

O termo "traço funcional" (*functional traits*, em inglês) tem inúmeras definições na literatura. Pode ser definido, em linhas gerais, como quaisquer atributos - sejam características morfológicas, bioquímicas, fisiológicas, estruturais, fenológicas ou comportamentais - que exerçam uma influência significativa no estabelecimento, sobrevivência e reprodução dos organismos, e que sejam expressas em fenótipos de organismos individuais, sendo estas consideradas relevantes para a resposta desses organismos ao ambiente e/ou seus efeitos nas propriedades do ecossistema (Díaz et al., 2013; Garnier et al., 2016; Reich et al., 2003; Violle et al., 2007).

A utilização de atributos funcionais permite organizar espécies ou indivíduos com funções ou respostas similares, *i.é*, cujos estados de atributos sejam semelhantes (Rosenfield & Müller, 2020). Os atributos funcionais podem ser classificados com base na relação atributo-ecossistema, em outros termos, se eles sofrem variação em resposta a mudanças ambientais ou se são capazes de afetar processos ecossistêmicos. Nesse sentido, os atributos funcionais podem ser denominados como atributos *resposta*, cujos valores ou estados se alteram em conformidade com características ambientais, ou atributos de *efeito*, que influenciam as funções ecológicas (Lavorel & Garnier, 2002; Rosenfield & Müller, 2020).

As plantas desenvolveram inúmeras estratégias no decorrer de suas histórias de vida para obterem sucesso em diversos ambientes da Terra. Entretanto, ainda são escassos os estudos voltados à compreensão da evolução por seleção natural dos traços funcionais de plantas ao longo de gerações (Caruso et al., 2020). No entanto, evidências demonstram padrões globais em relação às variações em plantas (Adler et al., 2014), tais como o espectro da economia da folha (Osnas et al., 2013; Wright et al., 2004) e da madeira (Chave et al., 2009) e a compensação entre tamanho e número de sementes (Moles & Westoby, 2006; Venable, 1992).

Por consequência, os atributos funcionais passaram a ser considerados como a melhor abordagem na compreensão geral preditiva de comunidades e ecossistemas (Adler et al., 2014). Graças à disponibilidade de informações em bases de dados globais, como o *TRY: Plant Trait Database* < https://www.try-db.org/> que contém cerca de 148.000 táxons de plantas e 6,9 milhões de registros de atributos (Kattge et al., 2020), e informações regionais (Rosenfield & Müller, 2020), as abordagens fundamentadas em atributos funcionais de plantas têm sido amplamente utilizadas (Adler et al., 2014) para predizer o resultado da assembleia de comunidades (Cornwell & Ackerly, 2009; Laughlin et al., 2012; Shipley et al., 2006), a dinâmica global da vegetação (Scholze et al., 2006) e a taxa dos processos ecossistêmicos (Díaz & Cabido, 2001; Eviner & Chapin III, 2003; Garnier et al., 2004; Lavorel & Garnier, 2002).

O conhecimento existente sobre atributos funcionais ainda se concentra em espécies de regiões temperadas (Carlucci et al., 2020; Hortal et al., 2015). Informações taxonômicas, ecológicas e fisiológicas básicas para um grande número de espécies nativas nos trópicos, bem como sobre atributos funcionais, ainda são ausentes (Aerts & Honnay, 2011), dificultando a recomposição de comunidades tropicais originalmente megadiversas (Carlucci et al., 2020). Apesar disso, a disponibilidade de dados atualmente permite compreender em certo nível como determinados atributos se associam a diferentes funções e estratégias ecológicas das plantas (*i.é*, espectros de características) (Díaz et al., 2016). Os atributos mais comumente medidos em plantas estão relacionados à aspectos foliares, reprodutivos, de crescimento e de raiz (Pérez-Harguindeguy et al., 2013; Rosenfield & Müller, 2020).

Nessa lógica, ao entendermos funções associadas a atributos funcionais, também compreendemos a história evolutiva das plantas, a formação e manutenção de comunidades, bem como os atributos que podem ser priorizados em ações de restauração visando a estruturação de comunidades com alta diversidade funcional. Ao separar as espécies em grupos funcionais, podem ser destacados os processos de maior interesse para as ações de restauração. A seleção de traços representa uma etapa importante, uma vez que certos traços funcionais podem responder a diferentes condições e recursos do ambiente, assim como provocar efeitos em processos ecológicos (Rosenfield & Müller,

2020).

Da perspectiva da restauração ecológica, o uso de atributos funcionais é considerado um desafio. É sabido que as trajetórias sucessionais são imprevisíveis e podem seguir múltiplas direções (Mesquita et al., 2015; Norden et al., 2015), tal qual a dinâmica dos ecossistemas de referência (Hiers et al., 2012) podem ser difíceis de prever ao longo do tempo. Além disso, uma espécie pode integrar mais que um grupo funcional e, desta forma, desempenhar diversas funções, em graus variados (Diaz et al., 2007), o que significa que seus diversos traços e múltiplos efeitos podem contribuir de forma independente ou conjunta no ecossistema (Carlucci et al., 2020; Gamfeldt et al., 2008).De acordo com Carlucci *et al.* (2020), as espécies acabam representando mais um *"continuum* multivariado" do que um cenário de espécies classificadas em grupos funcionais discretos.

As interações ecológicas, quando explicitamente vinculadas a atributos, podem ser quantificadas em diversos níveis de organização, de indivíduos até comunidades e ecossistemas (Díaz et al., 2016). Portanto, é fundamental escalonar atributos verificados em nível de organismo para outros níveis de organização, a fim de inferir ou compreender as funções que influenciam tais comunidades e ecossistemas (Rosenfield & Müller, 2020). Nesse sentido, mostram-se necessários estudos que forneçam informações sobre atributos vinculados a funções ecossistêmicas chave e que, dessa forma, possibilitem a definição de serviços e atributos funcionais prioritários para a restauração ecológica. É importante entender como atributos de efeito atuam na estruturação e manutenção da comunidade, garantindo a ela estabilidade e resiliência. Essas informações são imprescindíveis para a criação de estruturas quantitativas baseadas em atributos, que permitam a seleção de conjuntos de espécies nativas e suas abundâncias para áreas que estarão sujeitas a restauração. Além disso, ainda é necessário focar na obtenção de informações taxonômicas, ecológicas e fisiológicas básicas e de traços funcionais para espécies nativas de vegetações cujas características ainda são pouco conhecidas, como as Florestas Estacionais, por exemplo.

Esta tese apresenta o estudo de atributos funcionais de espécies arbustivas e arbóreas de Florestas Estacionais, um tipo de vegetação caracterizada pela sazonalidade (alternância de períodos chuvosos e secos) e pertencente ao domínio fitogeográfico da Mata Atlântica (Marques et al., 2021). Serão abordadas tanto as Florestas Estacionais Semideciduais, nas quais 20-50% das árvores perdem suas folhas no inverno, quanto as Florestas Estacionais Deciduais, onde mais de 50% das árvores perdem suas folhas no inverno (Marques et al., 2021), assim como Florestas de Transição para Savana Florestada ou para Floresta Ripícola.

Os capítulos desta tese foram redigidos em formato de artigos a serem submetidos a diferentes revistas, cada uma alinhada ao escopo de interesse dos estudos realizados (Appendix C). O

primeiro capítulo, que se concentra em mensurar o sinal filogenético dos traços e compreender as principais convergências e divergências funcionais entre as fitofisionomias de Florestas Estacionais, será submetido à revista "*Functional Ecology*", que tem foco na área de atributos funcionais e ecologia, incluindo temas relevantes como a evolução dos organismos em relação aos traços funcionais e fenômenos ecológicos em uma escala mais abrangente. Neste capítulo, é analisado quais traços foram mais conservados e quais são mais aleatórios ou superdispersos nessas florestas, bem como se existem diferenças significativas entre elas. Além disso, busca-se compreender se as relações filogenéticas revelam padrões de evolução para os diferentes traços funcionais nessas comunidades.

O segundo capítulo, que agrupa espécies em "*clusters*" com base em seus traços funcionais e analisa sua relação com fatores ambientais, será submetido à revista "*Journal of Applied Ecology*", que publica artigos na interface entre ciência ecológica e o manejo do ambiente natural, especialmente em relação à conservação da biodiversidade e à aplicação prática de conhecimentos ecológicos. Nesse segundo capítulo, é analisada a sobreposição e relação desses grupos funcionais em espaço multivariado. Verifica-se também se as espécies pertencentes a esses clusters apresentam distribuições espaciais diferentes ao longo do domínio fitogeográfico e se essas distribuições estão (ou podem estar) relacionadas a fatores ambientais, como clima, solo e geomorfologia. Por fim, discute-se como a a interação desses "*clusters*" com os fatores ambientais, em um contexto de mudanças ambientais, e se estes podem influenciar a estabilidade e dinâmica da comunidade, e como o manejo adequado desses "*clusters*" pode ser aplicado em programas de restauração ecológica. Desse modo, esse estudo pode fornecer informações até então inexistentes sobre atributos funcionais em Florestas Estacionais, e também pode avançar no entendimento teórico dos grupos funcionais, suas interações, suas influências no funcionamento das comunidades.

## **1** Presentation

This thesis explores the functional traits of shrub and tree species present in Seasonal Forests. This presentation conceptually describes functional traits, highlighting the ecological interactions and effects they may mediate, as well as the advantages and challenges of trait-based approaches. It also discusses how studying functional attributes can contribute to understanding plant evolutionary history, the formation and maintenance of communities, and providing support for large-scale ecological restoration in the tropics while addressing existing theoretical gaps. Finally, it contextualises functional approaches in Seasonal Forests and illustrates how this thesis can contribute to these advancements.

When we examine the evolutionary process of organisms throughout Earth's history, we observe a series of adaptive traits selected over their evolutionary paths. Such traits, resulting from a prolonged process of natural selection, have endowed organisms with the ability to survive, reproduce, and acquire resources in their environments. As these traits begin to influence an individual's growth, survival, and reproduction, and mediate their interactions with the environment, they can be regarded as attributes or functional traits (Caruso et al., 2020).

The term "functional trait" has numerous definitions in the literature. In general terms, it can be defined as any attribute—whether morphological, biochemical, physiological, structural, phenological, or behavioural—that significantly influences the establishment, survival, and reproduction of organisms and is expressed in the phenotypes of individual organisms, considered relevant to their response to the environment and/or their effects on ecosystem properties (Díaz et al., 2013; Garnier et al., 2016; Reich et al., 2003; Violle et al., 2007).

Using functional traits allows for the organisation of species or individuals with similar functions or responses—those whose trait states are alike (Rosenfield & Müller, 2020). Functional traits can be classified based on their attribute-ecosystem relationship, in other words, whether they vary in response to environmental changes or can affect ecosystem processes. In this context, functional traits can be termed response traits, whose values or states change according to environmental conditions, or effect traits, which influence ecological functions (Lavorel & Garnier, 2002; Rosenfield & Müller, 2020).

Plants have developed numerous strategies throughout their life histories to succeed in various environments on Earth. However, studies focused on understanding the natural selection-driven evolution of plant functional traits across generations are still scarce (Caruso et al., 2020). Nevertheless, evidence demonstrates global patterns regarding plant variations (Adler et al., 2014), such as leaf

economic spectrum (Osnas et al., 2013; Wright et al., 2004), wood density (Chave et al., 2009), and the trade-off between seed size and number (Moles & Westoby, 2006; Venable, 1992).

Consequently, functional traits have been considered the most promising approach in the overall predictive understanding of communities and ecosystems (Adler et al., 2014). Thanks to the availability of data in global databases, such as TRY Plant Trait Database <https://www.try-db.org/>, which contains about 148,000 plant taxa and 6.9 million trait records (Kattge et al., 2020), and regional information (Rosenfield & Müller, 2020), atrait-based approaches have been widely used (Adler et al., 2014) to predict community assembly outcomes (Cornwell & Ackerly, 2009; Laughlin et al., 2012; Shipley et al., 2006), global vegetation dynamics (Scholze et al., 2006), and the rate of ecosystem processes (Díaz & Cabido, 2001; Eviner & Chapin III, 2003; Garnier et al., 2004; Lavorel & Garnier, 2002).

Current knowledge on functional traits still primarily focuses on species from temperate regions (Carlucci et al., 2020; Hortal et al., 2015). Basic taxonomic, ecological, and physiological information for a large number of native species in the tropics, as well as information on functional traits, remains lacking (Aerts & Honnay, 2011), hindering the restoration of originally mega-diverse tropical communities (Carlucci et al., 2020). Nevertheless, the current availability of data enables an understanding, to some extent, of how certain traits are associated with different plant functions and ecological strategies (i.e., trait spectra) (Díaz et al., 2016). The most commonly measured plant traits relate to leaf, reproductive, growth, and root aspects (Pérez-Harguindeguy et al., 2013; Rosenfield & Müller, 2020).

In this framework, by understanding functions associated with functional traits, we also gain insight into plant evolutionary history, community formation and maintenance, as well as attributes that may be prioritised in restoration actions aimed at creating communities with high functional diversity. Grouping species into functional groups helps highlight processes of greater interest for restoration efforts. Trait selection represents an important step, since certain functional traits may respond differently to environmental conditions and resources, as well as affect ecological processes (Rosenfield & Müller, 2020).

From an ecological restoration perspective, the use of functional traits is still considered a challenge. Successional trajectories are known to be unpredictable and can follow multiple directions (Mesquita et al., 2015; Norden et al., 2015), just as reference ecosystem dynamics (Hiers et al., 2012) can be difficult to predict over time. Moreover, a species may belong to more than one functional group and thus perform various functions to varying degrees (Diaz et al., 2007), meaning their diverse traits and multiple effects can contribute independently or collectively to the ecosystem (Carlucci et al., 2020; Gamfeldt et al., 2008). According to Carlucci et al. (2020), species often represent more of a

"*multivariate* continuum" than a scenario of species classified into discrete functional groups.

Ecological interactions, when explicitly linked to attributes, can be quantified at various levels of organisation, from individuals to communities and ecosystems (Díaz et al., 2016). Therefore, scaling up verified organism-level traits to other levels of organisation is crucial for inferring or understanding the functions that influence such communities and ecosystems (Rosenfield & Müller, 2020). In this regard, studies are needed that provide information on attributes linked to key ecosystem functions and, thus, enable the identification of priority services and functional attributes for ecological restoration. It is essential to understand how effect traits operate in structuring and maintaining the community, ensuring its stability and resilience. This information is essential for creating quantitative frameworks based on attributes, allowing the selection of native species assemblages and their abundances for areas subject to restoration. Furthermore, there is still a need to focus on obtaining basic taxonomic, ecological, and physiological information and functional traits for native species of vegetation whose characteristics are still poorly understood, such as Seasonal Forests, for example.

This thesis presents the study of functional traits of shrub and tree species in Seasonal Forests, a type of vegetation characterised by seasonality (alternation of rainy and dry periods) and belonging to the phytogeographic domain of the Atlantic Forest (Marques et al., 2021). Both Semi-deciduous Seasonal Forests, where 20-50% oof trees lose their leaves in winter, and Deciduous Seasonal Forests, where more than 50% of trees lose their leaves in winter (Marques et al., 2021), as well as Transition Forests to Forested Savannah or Riparian Forests, will be addressed.

The chapters of this thesis are written in the format of articles to be submitted to different journals, each aligned with the scope of the studies conducted (Appendix C). The first chapter, which focuses on measuring the phylogenetic signal of traits and understanding the main functional convergences and divergences among the phytophysiognomies of Seasonal Forests, will be submitted to the journal "*Functional Ecology*", which focuses on functional traits and ecology, including relevant topics such as organism evolution alongside functional traits and ecological phenomena on a broader scale. This chapter analyses which traits are more conserved and which are more random or overdispersed in these forests, and whether there are significant differences among them. Additionally, it seeks to understand whether phylogenetic relationships reveal evolutionary patterns for different functional traits in these communities.

The second chapter, which groups species into clusters based on their functional traits and examines their relationship with environmental factors, will be submitted to the journal "*Journal of Applied Ecology*", which publishes articles at the interface between ecological science and natural

resource management, particularly concerning biodiversity conservation and the practical application of ecological knowledge. This second chapter analyses the overlap and relationship of these functional groups in multivariate space. It also examines whether the species within these clusters exhibit different spatial distributions across the phytogeographic domain and whether these distributions are (or could be) related to environmental factors such as climate, soil, and geomorphology. Finally, it discusses how the interaction of these clusters with environmental factors, in the context of environmental changes, might influence community stability and dynamics and how proper management of these clusters can be applied in ecological restoration programmes. Thus, this study could provide previously unavailable information on functional attributes in Seasonal Forests and advance theoretical understanding of functional groups, their interactions, and their influences on community functioning.

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## **Chapter 1**

## The traits phylogeny and its effects on the multifunctional structure of Brazilian's Seasonal Forests

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#### **Funding information**

Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES)

#### ABSTRACT

1. Functional traits are aspects of organisms that influence their establishment, survival, and reproduction, responding to environmental conditions and affecting ecosystem properties. The study of functional traits is crucial for understanding the structuring of plant communities and biological diversity in different environments.

2. We evaluated ten functional traits relevant to plant fitness in three types of Seasonal Forests in Mato Grosso do Sul, Brazil. We used *D* statistics to estimate phylogenetic signal and Correspondence Analysis (CA) to explore patterns in the associations between variables.

3. Each type of forest exhibited different degrees of phylogenetic conservation for each trait, indicating the influence of specific environmental and evolutionary factors in each context, providing insights into how such factors have shaped the evolution of plant communities in different forest ecosystems.

4. Flower size and dispersal syndrome were the conserved traits in the three forests examined, reflecting the close relationship between plants and pollinating and seed-dispersing organisms over evolutionary time.

5. Spinescence was characterised as an overdispersed trait in the Semideciduous Forests, as well as resprouting capacity, which was overdispersed in the Semideciduous and Transition Forests but random in the Deciduous Forests. This highlights the adaptation of plants to selective pressures related to disturbances such as cutting, herbivore grazing, or wildfires.

6. *Synthesis and applications*. The results demonstrate that different traits have evolved in distinct ways in the three forests analysed. Some traits are more conserved in one or more forests, while others are more random or dispersed. Correspondence Analysis (CA) satisfactorily explained the variance of functional traits along the dimensions of the biplot, capturing a significant portion of the total data variability. Our findings provide valuable insights into how functional traits can be used to understand the structure and dynamics of plant communities in different forest ecosystems.

## **KEYWORDS**

functional traits, phylogenetic conservation, phylogenetic signal, seed dispersers, plant adaptation, seasonal forests, evolution of plant communities

## A filogenia dos traços e seus efeitos na estrutura multifuncional em Florestas Estacionais

#### Larissa Oliveira Vilela

#### RESUMO

1. Traços funcionais são aspectos dos organismos que influenciam seu estabelecimento, sobrevivência e reprodução, respondendo às condições ambientais e afetando as propriedades do ecossistema. O estudo dos traços funcionais é crucial para entender a estruturação das comunidades vegetais e a diversidade biológica em diferentes ambientes.

2. Avaliamos dez traços funcionais relevantes para a aptidão das plantas em três tipos de Florestas Estacionais em Mato Grosso do Sul. Utilizamos a estatística *D* para estimar o sinal filogenético e a Análise de Correspondência (CA) para explorar padrões nas associações entre as variáveis.

3. Cada tipo de floresta exibiu diferentes graus de conservação filogenética para cada traço, indicando a influência de fatores ambientais e evolutivos específicos em cada contexto, fornecendo subsídios para entender como tais fatores moldaram a evolução das comunidades vegetais em diferentes ecossistemas florestais.

4. O tamanho da flor e a síndrome de dispersão foram os traços conservados nas três florestas examinadas, refletindo a estreita relação entre plantas e organismos polinizadores e dispersores de sementes ao longo do tempo evolutivo.

5. A espinescência foi caracterizada como um traço superdisperso nas Florestas Semidecíduas, assim como a capacidade de rebrota, superdispersa nas Florestas Semidecíduas e de Transição, mas aleatória nas Florestas Decíduas, destacando a adaptação das plantas a pressões seletivas relacionadas à distúrbios como corte, pastoreio de herbívoros ou incêndios florestais.

6. *Síntese e aplicações.* Os resultados demonstram que diferentes traços evoluíram de maneiras distintas nas três florestas analisadas. Alguns traços são mais conservados em uma ou mais florestas, enquanto outros são mais aleatórios ou dispersos. A Análise de Correspondência (CA) explicou satisfatoriamente a variância dos traços funcionais ao longo das dimensões do biplot, capturando uma parcela significativa da variabilidade total dos dados. Os nossos achados fornecem *insights* valiosos sobre como os traços funcionais podem ser usados para entender a estrutura e a dinâmica das comunidades vegetais em diferentes ecossistemas florestais.

#### PALAVRAS-CHAVE

traços funcionais, conservação filogenética, sinal filogenético, dispersores de sementes, adaptação das plantas, florestas estacionais, evolução das comunidades vegetais.

#### 1 Introduction

The discussion on species distribution patterns and biological diversity in natural communities has been extensively explored for decades (Brown, 1995; Clements, 1916; Fisher et al., 1943; Gleason, 1927; MacArthur, 1960; MacArthur & Wilson, 1967; Preston, 1948). Comprehending the processes that drive variations in species composition, diversity, and abundance of competing species has been a key objective in Ecology (Kraft et al., 2007). Although it is known that the distribution of plants and their functional traits is not random (Cody & Diamond, 1975; Raunkiær, 2015), there is still limited knowledge about the mechanisms determining species composition in a community (Valladares et al., 2008). Significant gaps persist, such as the need to integrate functional traits and environmental factors (Hu et al., 2021; Holdaway et al., 2011), intra- and interspecific variation in traits (Kichenin et al., 2013), and the importance of interactions with soil microorganisms (Bever et al., 2010; Jíménez-Alfaro et al., 2016). According to Webb et al. (2002), many communities display non-random patterns of evolutionary relatedness among the species that comprise them, due to the interaction between phylogenetically conserved or convergent functional traits and ecological processes, such as environmental filters or competitive exclusion.

Functional traits are aspects of organisms capable of influencing their establishment, survival, and reproduction, as well as responding to environmental conditions and affecting ecosystem properties (Díaz et al., 2013; Garnier et al., 2016; Reich et al., 2003; Violle et al., 2007). Leaf, reproductive, growth, and root traits are most commonly measured in plants (Kattge et al., 2020; Pérez-Harguindeguy et al., 2013; Rosenfield & Müller, 2020). Recently, plant functional ecology has expanded the spectrum of investigated functional traits, including belowground traits related to root economics (Carmona et al., 2021; Kramer-Walter et al., 2016; Weemstra et al., 2016), carbohydrate storage (Lubbe et al., 2021), mycorrhizal symbiosis (Bergmann et al., 2020), and floral and reproductive traits (E-Vojtkó et al., 2022; Roddy et al., 2019; Segrestin et al., 2020).

The comparison of functional traits and organism fitness primarily addresses ecological scales and processes, rather than evolutionary ones (Laughlin et al., 2020). However, the evolution of traits is expressed along the branches of organism phylogeny (Díaz et al., 2013), and the coordinated variation of functional traits in plants is manifested in correlations that reflect their shared evolutionary history (Kleyer & Minden, 2015; Murren, 2002, 2012). Evolutionarily related species tend to be ecologically similar and respond similarly to the selection, resulting in more similar values of functional traits in these species compared to those with distant relatedness and, therefore, showing phylogenetic signal (Ackerly, 2009; Freckleton et al., 2002; Harvey & Pagel, 1991). Thus, phylogenetic signal, i.e., the distribution of a functional trait among the species composing a community, can elucidate shared

evolutionary history and help understand the processes that have shaped the spatial distribution of species over time.

In this context, our objective is to understand the evolutionary mechanisms associated with the development of functional traits in the woody flora of three different types of Seasonal Forests. By considering both phylogenetic information and the functional traits of species, we aim to address several key questions: Which traits are more conserved, and which are more random or overdispersed in each type of forest? Are there significant differences in the evolutionary patterns of these communities for different functional traits? What are the functional convergences and divergences among vegetation types? Are there correlations or associations among the evaluated traits? This information can contribute to a better understanding of how plant communities are structured and how different evolutionary and ecological factors may impact species composition and biodiversity in various environments. Our investigation is guided by two main hypotheses. First, we hypothesize that certain functional traits, particularly those related to plant-fauna interactions, exhibit signs of phylogenetic conservatism. Second, we predict that traits associated with resistance to disturbances —such as climate change, herbivory, and other environmental stresses— will show overdispersion in Seasonal Forests, reflecting the intense selective pressures present in these environments.

To test these hypotheses, we selected and collected data on ten essential functional traits for plant fitness, including leaf characteristics, spatial occupation, reproductive traits, floral traits, and survival attributes of the woody flora in three types of Seasonal Forests in the state of Mato Grosso do Sul. We used the D statistic (Fritz & Purvis, 2010) to estimate the phylogenetic signal, providing a deeper understanding of how these traits are distributed across the phylogeny of the studied species. Additionally, we employed Correspondence Analysis to explore and identify association patterns between variables, aiming to elucidate how such patterns vary among different forest types. The findings allowed us to understand that different forest types exhibit distinct patterns of phylogenetic conservation for various traits and provided insights into how historical and environmental factors have shaped the evolution of plant communities in different forest ecosystems.

### 2 Material and Methods

#### 2.1 Data sources

We compiled data from 470 species, including trees, shrubs, cacti, and palms, listed by Damasceno-Junior et al. (2018) for the state of Mato Grosso do Sul, to gather the functional traits of woody species in Seasonal Forests. The species were classified based on their occurrence records in different phytophysiognomies, which include Deciduous Seasonal Forest, Semideciduous Seasonal Forest, and Transition to Forested Savanna or Riparian Forest (referred to here as Transition Forest), as described by Damasceno-Junior et al. (2018). The plant families were classified according to the Angiosperm Phylogeny Group (APG IV, 2016), and botanical nomenclature was standardised according to the Flora e Funga do Brasil (2023) <floradobrasil.jbrj.gov.br>.

To obtain information on the functional traits of species within this assemblage, we collected data from various sources, including the TRY - Plant Trait Database <try-db.org> (Kattge et al., 2020), the BIEN - Botanical Information and Ecology Network database <bien.nceas.ucsb.edu/bien>, the CRIA - Centro de Referência em Informação Ambiental <cria.org.br> and the GBIF - Global Biodiversity Information Facility. Additionally, we sought information from the bibliographic sources listed in Supporting Information Table S1 for species lacking trait data in the databases above.

## **2.2 Functional Plant Traits**

We considered only those that exhibited ecological relevance to select the functional traits that would impact plant fitness (Violle et al., 2007), as demonstrated in Table 1. In total, we selected ten traits, five of which were related to leaf characteristics and spatial occupation of the plants (such as the size of the adult plant (Hmax), stem specific density (SSD), vegetative phenology, leaf epidermal characteristics, and spinescence), four related to reproductive and floral characteristics (such as flower size and colour, pollination type, and dispersal syndrome), and one related to survival (plant resprouting capacity).

Traits	Ecological significance	References
Size of the adult plant (Hmax)	Positively related to competitive ability (competition for light)	(E-Vojtkó et al., 2022)
Stem-specific density (SSD) or wood density (g.cm-3)	Climatic change resistance (drought resilience)	(Carlucci et al., 2020; Hacke et al., 2001; Laughlin, 2014)
Vegetative phenology	Reduction of herbivory and less loss of water and nutrients during drought	(Pringle et al., 2011)
Leaf epidermal characteristics	Climatic change resistance (protective function to high solar radiation and high temperatures)	(Moles et al., 2020)
Spinescence	Reduction of herbivory	(Hanley et al., 2007; Xu et al., 2020)
Flower size	Pollinator attraction and flower production cost	(Krizek & Anderson, 2013)
Flower colour	Pollinator attraction and flower production cost	(E-Vojtkó et al., 2022)
Pollination type	Related to pollinator dependency	(E-Vojtkó et al., 2022)
Disportal syndroma	Delated to dispersal forms dependency	(Pijl, 1982; van Rheede van
Dispersal synuronne		Oudtshoorn & van Rooyen, 1999)
Plant resprouting capacity	Disturbance resistance (fire resistance)	(Clarke et al., 2013; Moris et al., 2022)

 Table 1. Functional traits used in the analyses and their ecological significance.

### 2.3 Data analyses

We employed the "phylo.maker" function from the "V.PhyloMaker2" library (Jin & Qian,

2022) in the R software to generate phylogenetic trees for the species lists (Figure 1) and to understand the evolutionary relationships among the species. To estimate the phylogenetic signal, we utilised the *D* statistic (Fritz & Purvis, 2010), a metric developed to measure phylogenetic signal in binary data through the "phylo.d" function in the R-package "Caper" (Orme et al., 2018). The sum of changes in the estimated nodal values of a binary trait in a phylogeny (*D*) provides a measure of the phylogenetic signal for that trait (Fritz & Purvis, 2010).



C. Transitional forest





The "phylo.d" function tests the estimated D value for significant distances in a random association and the expected clustering under the Brownian threshold evolution model. In other words, calculate the observed D for an attribute in a tree and compare it with the value of D found using the same number of simulations for the phylogenetic randomness model, where the trait values are randomly shuffled concerning the phylogeny tips and D is calculated; and for the Brownian threshold model, where a continuous attribute is developed along the phylogeny under a Brownian process and

then converted into a binary attribute using a threshold that reproduces the relative prevalence of the observed trait. D values equal to 0 indicate a more clustered phylogenetic structure according to the Brownian threshold model, while values equal to 1 indicate a random phylogenetic distribution at the tips of the phylogeny (Fritz & Purvis, 2010). D values can also fall outside this range. When less than 0 (D < 0), they suggest that the trait is highly phylogenetically conserved, while values greater than 1 (D > 1) indicate that the trait is more overdispersed than expected by chance (Fritz & Purvis, 2010). Functional trait values were transformed into binary values according to their positive or negative relationship with their ecological significance (Table 2). Information on missing traits in the data table was excluded from the analysis using the "na.omit" function.

**Table 2.** Summary representation of the functional traits used in further analyses by transforming their values into a binary scale based on their ecological significance.

Low-value interpretation	Trait name	High-value interpretation
0. small	Size of the adult plant (Hmax)	1. medium and/or large
0. light woods and/or moderately dense woods	Stem-specific density (SSD) or wood density (g.cm-3)	1. dense woods and/or very dense woods
0. semi-deciduous and/or deciduous	Vegetative phenology	1. evergreen
0. glabrous	Leaf epidermal characteristics	1. hispid, lanate or very tomentose
0. not spiny	Spinescence	1. spiny
0. small and/or intermediate	Flower size	1. big
0. greenish	Flower colour	1. white or coloured
0. wind and/or water pollination	Pollination type	1. animal pollination
0. anemochorous and/or autochorous	Dispersal syndrome	1. zoochorous
0. absence	Plant resprouting capacity	1. presence or ambiguous

To explore and visualise the associations between categories of categorical variables in a low-dimensional space and identify patterns in the associations between the variables, we used Correspondence Analysis (CA). CA is a multivariate analysis instrumental when dealing with binary, nominal, or ordinal variables and when there are many cells in the contingency table dataset (Beh & Lombardo, 2014; Greenacre, 2017). We performed Correspondence Analysis on datasets from the three types of Seasonal Forests (Deciduous Forest, Semideciduous Forest, and Transitional Forest), using the R-package "FactoMineR" (Lê et al., 2008) for the "CA" function and the R-package "ggplot2" (Wickham, 2016) for the "plot.CA" function in the R software. The "CA" function calculates the contribution values of each species and each variable (or functional trait) and their associations. Before the analysis, the "na.omit" function was applied to remove any missing values in the data table. The chi-square test was performed to determine the presence or absence of statistically significant associations between the variables. All analyses mentioned above were conducted using the statistical software R version 4.1.1 (R Core Team, 2021) and RStudio Team (2022).

## **3 Results**

We found that each type of forest exhibits different degrees of phylogenetic conservation for each trait, indicating the influence of specific environmental and evolutionary factors in each context, as detailed in Supporting Information Table S2 and Figure 2.



**Figure 2.** Estimated D values for each trait across three physiognomies of the seasonal forest. *D*-values, Fritz and Purvis's *D* (Fritz & Purvis, 2010). Values of *D* may range from <0 (highly conserved) to 0 (conserved according to the Brownian threshold model), to 1 (random), to >1 (overdispersed).

Regarding the analysed traits, it was observed that adult plant size (Hmax) showed moderate values of phylogenetic conservation for Transitional Forests (0,4540655) and more random values for Deciduous Forests (0,7571172) and Semideciduous Forests (0,9714001), suggesting that this characteristic is more conserved in Transitional Forests and more dispersed in the other two phytogeographic formations. Wood density (SSD) presented values greater than 1 for the Transitional Forest (1,028679) and close to 1 for the Deciduous Forest (0,7734552), indicating the random evolution of this trait. On the other hand, for the Semideciduous Forest, the value of SSD was less than 1 (0,5691683), suggesting that wood density is more conserved in this forest than in the others.

Regarding leaf traits, it was observed that leaf phenology and leaf epidermal characteristics (Leaf\_cha) were more conserved in Semideciduous Forests than in the others, while spinescence proved to be an overdispersed trait. Leaf phenology was more random in Deciduous (1,060419) and Transitional Forests (0,8654366) but more conserved in Semideciduous Forests (0,4238272). The Leaf\_cha trait had a value close to 1 and, therefore, more random in Transitional Forests (1,010963) and lower values in

Deciduous (0,6480734) and Semideciduous Forests (0,3911315). As for spinescence, this trait showed a moderate degree of phylogenetic conservation in Deciduous (0,3887693) and Transitional Forests (0,538733) but was overdispersed in Semideciduous Forests (1,313996).

The floral traits exhibited significant variations concerning the D values. Among them, flower size was one of the most conserved traits. The analysis demonstrated that flower size is highly conserved in Deciduous Forests (-0,1930143), while in Semideciduous Forests (0,0719513) and Transition Forests (0,2649111), it showed a degree of phylogenetic conservation. Regarding flower colour, values close to 0.5 were observed for Semideciduous Forests (0,6517187), and Transition Forests (0,5806129), and a D value closer to 0 was found in Deciduous Forests (0,2011635), indicating that, like size, flower colour is also more conserved in Deciduous Forests. Pollination showed the most disparate values among all traits, being highly conserved in Semideciduous Forests (-0,8589665) and Deciduous Forests (-1,200868) and overdispersed in Transition Forests (2,378267).

Finally, dispersal syndrome was conserved in Semideciduous Forests (0,3187124) and highly conserved in Deciduous Forests (-0,0200040) and Transition Forests (-0,1433094). On the another hand, resprouting capacity was found to be random in Deciduous Forests (0,7968552) and overdispersed in Semideciduous Forests (1.223328) and Transition Forests (1,073293). The results show that different traits evolved differently in the three analysed forests (Table S2, Figure 2). Some traits are more conserved in one or more forests, while others are more random or overdispersed.

The Correspondence Analysis (CA) results satisfactorily explained the variance of the functional traits along the biplot dimensions (Figure 3). In Deciduous Seasonal Forests, the cumulative percentage of variance explained by Dim.1 and Dim.2 together accounted for 34.518% of the total variation, capturing over one-third of the total data variability. In Semideciduous Seasonal Forests, Dim.1 and Dim.2 together explained 35.946% of the total variation. The cumulative percentage of explained variation when considering Dim.3 was 51.172%, showing the same results. In Transition Forests, Dim.1 and Dim.2 explain 39.665% of the total variation, while the first four dimensions (Dim.1 to Dim.4) explain 65.856%. From the fifth dimension onwards, the explained variation decreases significantly (Table S3).



**Figure 3.** Correspondence Analysis (CA) factor map demonstrating the associations between variables for the three phytophysiognomies of the seasonal forest. The colour gradient represents the contribution of the variables.

The Correspondence Analysis (CA) plot depicts the correlations between variables within each vegetation type (Figure 3). Across all three phytophysiognomies, the relationship between variables and the dimensions of data variability in CA was similar. Among all environments, spinescence exhibited the highest relative contribution to the total data variability and played a crucial role in sample differentiation (Table S3). Traits such as SSD (Specific Leaf Area) and flower size also displayed high inertia values. Conversely, traits such as pollination, flower colour, and dispersal syndrome had lower relative contributions to the CA dimensions. The obtained chi-square test values for independence were 537.5066, 709.8971, and 408.6947, with p-values equal to 1 in all cases for Deciduous Seasonal Forests, Semi-deciduous Seasonal Forests, and Transition Forests, respectively. This result suggests that, at the significance levels considered, there is insufficient statistical evidence to claim that functional traits are dependent on one another.

#### 4 Discussion

The phylogenetic signal of functional traits reflects the shared evolutionary history between species and their traits, demonstrating that certain traits are more important than others for the survival and adaptation of plants in specific environments (Cronk, 2004; Gurevitch et al., 2006). Our results indicate that functional traits of the studied plant assemblages differ regarding their phylogenetic clustering (Figure 2), having evolved in distinct and independent ways in the three examined forest ecosystems (Table S3). Some traits are more conserved in one or more forests, while others exhibit greater randomness or overdispersion.
The interpretation of the results support the formulated hypotheses. We identified significant phylogenetic conservation in traits such as flower size and dispersal syndromes, while characteristics such as spinescence and resprouting ability showed overdispersion patterns. These differences can shed light on how historical and environmental factors have shaped the evolution of these communities over time (Swenson et al., 2012; Webb et al., 2008).

A functionally conserved or highly conserved trait demonstrates that its evolution has occurred similarly in closely related phylogenetic species, and the evolution of this trait is influenced by both the shared evolutionary history among species and environmental filtering through abiotic factors (Bose et al., 2019; Helmus & Ives, 2012; Mayfield & Levine, 2010; Qian et al., 2014, 2017; Whitfeld et al., 2012). Analysis of the obtained *D* values (Figure 2) revealed that different types of forests exhibit distinct patterns of phylogenetic conservation for different traits. Flower size and dispersal syndrome were the most widely conserved traits in the three examined forests, suggesting that they play an important role in the survival and reproduction of the plant species present. This finding highlights the close relationship between plants and other organisms that play crucial roles in their evolution, such as pollinators and seed dispersers.

Correspondence Analysis (CA) revealed that flower size was also a significant and informative trait in the data structure (Figure 3), despite the absence of a significant relationship among the variables (Table S3). Flower size is a crucial characteristic in ecological contexts, as it impacts both the evolution and effectiveness of plant reproductive systems (Goodwillie et al., 2010; Krizek & Anderson, 2013; Sargent et al., 2007). This characteristic is significant because larger flowers generally contain more nectar and are more visible to pollinators (Blarer et al., 2002; Fenster et al., 2006). In plants that rely on cross-pollination, floral traits such as flower size are presumed to coevolve with pollinators (Goodwillie et al., 2010; Krizek & Anderson, 2013).

Regarding the dispersion syndrome, the observed conservatism indicates a tight relationship between dispersers and fruits that, throughout evolutionary time, has led to morphological convergences among plant species (Pijl, 1982). The evolution of fruit characteristics is highly responsive to mutualistic interactions with seed-dispersing frugivores - Seed Dispersal Syndrome Hypothesis (Valenta & Nevo, 2020). The high level of integration revealed by phylogenetic contrasts demonstrates that mutualistic frugivores can shape the phenotypic covariance of fleshy fruits (Valido et al., 2011), highlighting the conservatism of the phylogenetic niche (Crisp & Cook, 2012) and the importance of these interactions in the evolution of fleshy fruits and seed dispersal patterns.

Phylogenetic conservatism can indicate the presence of shared adaptations among closely related species under specific conditions, thus referred to as niche conservatism (Crisp & Cook, 2012;

Harvey & Pagel, 1991; Ricklefs, 2010; Webb et al., 2002). This phenomenon can be reinforced by the coexistence of closely related species in a physically stressful habitat, suggesting low competition for specific adaptations (Bruun et al., 2006; Callaway et al., 2002; Mienna et al., 2020). When species lineages tend to maintain their ecological niche-related traits over time, even after speciation events, it is referred to as the phenomenon of phylogenetic niche conservatism (Ackerly, 2003; Cooper et al., 2010; Crisp & Cook, 2012; Wiens et al., 2010). There is a debate in the literature as to whether phylogenetic niche conservatism is a process that structures communities and biomes or a pattern resulting from underlying causes, whether intrinsic or extrinsic (Crisp & Cook, 2012; Losos, 2008a, 2008b, 2011; Wiens & Graham, 2005). Wiens et al. (2010) argue that phylogenetic niche conservatism is a process because it can lead to other patterns, such as diversity gradients. However, the same processes may lead to phylogenetic niche conservatism and also generate other patterns (Cooper et al., 2010; Losos, 2011).

The type of pollination has also proven to be a highly conserved trait for Semideciduous Seasonal Forests and Deciduous Forests. This result suggests that, under the specific conditions of these particular forests, phylogenetically close species share adaptive similarities regarding the type of pollination, making this characteristic an important factor in the shared evolution of these species. In contrast, in Transition Forests, the type of pollination was an overdispersed trait. Unlike phylogenetic conservatism, which suggests the selection of species with similar traits and shared evolutionary histories due to abiotic factors and mild selective pressures (Bose et al., 2019; Helmus & Ives, 2012; Mayfield & Levine, 2010; Qian et al., 2014, 2017; Whitfeld et al., 2012), overdispersion is often associated with interspecific interactions, including competitive exclusion (Cavender-Bares et al., 2009; Webb et al., 2002) or facilitation (Valiente-Banuet & Verdú, 2007), as well as strong selective pressures or environmental filtering of ecologically important traits (Cavender-Bares et al., 2004; Das & Ratnam, 2022; Webb et al., 2002). Regarding pollination, the combination of interspecific facilitation and intra-specific competition among plants may promote their coexistence, suggesting that pollination can be a crucial factor in maintaining plant diversity as a niche axis, benefiting rare species and biodiversity maintenance (Bergamo et al., 2002; Feldman et al., 2004).

When a trait displays random or overdispersed patterns, that is, it exhibits a low degree of phylogenetic aggregation (Webb et al., 2002), phylogenetically distant species may possess similar characteristics (Münkemüller et al., 2012; Pavoine & Ricotta, 2013). Low-stress abiotic environments, characterised by greater habitat heterogeneity and significant dispersal constraints, can contribute to an increase in overdispersion, which occurs when multiple functional groups or distinct evolutionary lineages are simultaneously present (Butterfield et al., 2013; Dias et al., 2020; Mienna et al., 2020; Wang et al., 2013). Compared to others, a higher diversity of overdispersed traits in Transition Forests demonstrates that this forest exhibits a wide range of ecological environments with different selective

pressures, leading to a greater diversity of adaptive mechanisms among species.

In the Semideciduous Seasonal Forest, thorns in plants were an overdispersed characteristic that may have evolved as a defence mechanism and adaptation to avoid herbivory or protect leaves from large animals that feed on trees (Xu et al., 2020). It is essential to highlight that plant consumption by herbivorous mammals is one of the main factors driving vegetation dynamics worldwide (Huntly, 1991), which justifies its importance in the data structure for all forests evaluated by Correspondence Analysis (Figure 3). Furthermore, herbivorous mammals also exert an influence on the characteristics of plant thorns, such as their length, density, and distribution (Goheen et al., 2007; Karban & Myers, 1989; Young et al., 2003; Zhang et al., 2022).

Historical herbivory patterns explain a substantial portion of the current biogeographic variability in plant functional traits and ecosystem geographical distribution, highlighting the importance of the historical distribution of extinct neotropical megafauna in understanding the functional biogeography of plants and ecosystems (Dantas & Pausas, 2022). Although most of these animals were extinct by the end of the Pleistocene and the beginning of the Holocene (Owen-Smith, 2013), woody plants in herbivory-sustained ecosystems have developed morphological and physiological adaptations to minimize damage caused by large herbivores, known as anti-herbivory defense traits (Dantas & Pausas, 2020). Even though many of these traits have been lost in areas where selective pressure changed after megafauna extinction, some may have persisted as anachronistic features (Galetti et al., 2009; Janzen & Martin, 1982).

The resprouting capacity of plants was also an overdispersed characteristic in Semideciduous and Transitional Forests, appearing to be random in Deciduous Forests. Resprouting capacity is an extremely important trait whose different mechanisms have also emerged in response to strong selective pressures throughout the evolutionary history of plants, being closely linked to the plant's ability to recover after suffering damage caused by cutting, herbivore grazing, or wildfires (Clarke et al., 2013). Trees and shrubs possess resprouting mechanisms that allow them to regenerate tissues from buds in different plant parts, such as roots, stems, and branches (Clarke et al., 2013). Resprouting can vary significantly among plant species, influenced by physiological and genetic characteristics and factors such as the intensity and frequency of disturbances (Pausas & Keeley, 2014). Particularly in these forests, where wildfires are common, resprouting capacity is essential for plant survival (Abreu et al., 2022).

Our findings provide insights into understanding how historical and environmental factors have shaped the evolution of plant communities in different types of forest vegetation. The independence between traits and the relevance of certain functional traits over others for plant survival and adaptation in specific environments become evident. Additionally, distinct patterns of phylogenetic conservation for different traits were observed among the analysed forests. The traits most conserved across the three forests were flower size and dispersal syndrome, highlighting the inherent conservatism in the close relationship between plants, pollinators and seed dispersers, which play crucial roles in plant evolution.

The origins of the discrepant differences regarding the values found for the type of pollination need to be further studied, considering that the portion of the Atlantic Forest located in the state of Mato Grosso do Sul has recently been identified as a priority area for the protection of pollination networks and species interaction webs, which are essential for the survival and balance of ecological communities (Pereira et al., 2022). Moreover, the overdispersion found for spinescence in Semideciduous Seasonal Forests and for resprouting capacity indicates the solid selective pressure exerted by herbivory, cutting, or fire in these environments. These findings are consistent with the patterns of overdispersion described in the literature (Cavender-Bares et al., 2004; Das & Ratnam, 2022; Webb et al., 2002). The methodology presented here may be applied to explore other communities, enabling the expansion of knowledge about the complex interactions between evolutionary history, environmental filtering, and variation in functional traits, as well as mechanisms of coexistence and biodiversity maintenance in ecological communities.

# **5** Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. We thank Dr. Fátima C. M. Piña-Rodrigues and Dr. Sandro M. Silva for their friendly suggestions and comments on early versions of the manuscript.

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# **Supporting Information**

Table S1. Literature from which additional functional trait information was obtained.

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Trait name	Deciduous forest	Semideciduous forest	Transitional forest	
Hmax	0,7571172	0,9714001	0,4540655	Ì
SSD	0,7734552	0,5691683	1,028679	
Phenology	1,060419	0,4238272	0,8654366	
Leaf_cha	0,6480734	0,3911315	1,010963	
Spinescence	0,3887693	1,313996	0,538733	
Flower_size	-0,1930143*	0,0719513	0,2649111	
Flower_color	0,2011635	0,6517187	0,5806129	
Pollination	-1,200868*	-0,8589665*	2,378267	
Dispersal_syn	-0,0200040*	0,3187124	-0,1433094*	
Resprouting	0,7968552	1.223328	1,073293	

Table S2. Estimated D values for each trait across three physiognomies of the seasonal forest.

*Note*: Functional distances between species were calculated separately for each characteristic. Values marked by an asterisk (\*) denoting highly phylogenetically clustered traits.



**Figure S1.** Correspondence Analysis (CA) factor map demonstrating the associations between variables and species for the three phytophysiognomies of the seasonal forest. The colour gradient represents the contribution of the variables.

Table S3. Correspondence Analysis (CA) results across three physiognomies of the seasonal forest.

# **Deciduous forest**

The chi-square of independence between the two variables is equal to 537.5066 (p-value = 1).

Eigenvalues	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9	
Variance	0.227	0.209	0.195	0.171	0.134	0.116	0.097	0.092	0.022	
%ofvar.	17.961	16.557	15.417	13.572	10.602	9.221	7.675	7.272	1.723	
Cumulative%ofvar.	17.961	34.518	49.935	63.507	74.109	83.330	91.005	98.277	100.000	
Rows(the10first)	Iner*1000	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
Astronium_urundeuva	10.734	-0.100	0.052	0.011	-0.246	0.341	0.066	0.741	3.310	0.600
Schinopsis_brasiliensis	13.642	-0.158	0.077	0.013	-0.576	1.117	0.171	0.875	2.775	0.396
Annona_coriacea	12.120	-0.056	0.013	0.002	0.694	2.164	0.373	0.064	0.020	0.003
Annona_cornifolia	10.682	-0.236	0.345	0.073	0.636	2.724	0.533	-0.196	0.278	0.051
Annona_emarginata	16.735	-0.042	0.006	0.001	0.742	1.855	0.232	-0.113	0.046	0.005
Annona_nutans	11.922	-0.220	0.252	0.048	0.496	1.382	0.242	-0.300	0.545	0.089
Aspidosperma_cuspa	19.851	-0.417	0.540	0.062	-0.850	2.435	0.256	0.327	0.386	0.038
Aspidosperma_polyneuron	9.929	-0.175	0.127	0.029	-0.161	0.116	0.024	-0.095	0.044	0.009
Aspidosperma_subincanum	11.340	-0.213	0.236	0.047	-0.568	1.812	0.334	0.465	1.304	0.224
Aspidosperma_tomentosum	12.445	-0.434	0.977	0.178	0.251	0.355	0.060	-0.371	0.831	0.130

Deciduous forest										
Columns	Iner*1000	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
Hmax	115.010	0.135	0.940	0.019	-0.383	8.262	0.150	0.331	6.593	0.112
SSD	161.047	-0.175	0.855	0.012	-1.014	31.203	0.405	0.881	25.310	0.306
phenology	136.139	-0.417	5.588	0.093	-0.135	0.635	0.010	-0.776	22.515	0.322
leaf_cha	131.915	-0.149	0.756	0.013	0.610	13.789	0.218	0.144	0.830	0.012
Spinescence	208.192	2.852	84.277	0.917	0.178	0.357	0.004	-0.198	0.471	0.004
Flower_size	150.461	-0.194	0.898	0.014	1.218	38.370	0.533	0.443	5.456	0.071
Flower_color	80.362	-0.047	0.157	0.004	0.251	4.819	0.125	0.263	5.658	0.137
pollination	22.669	-0.003	0.001	0.000	-0.026	0.074	0.007	0.014	0.024	0.002
dispersal_syn	107.175	0.137	1.108	0.023	-0.175	1.962	0.038	-0.607	25.356	0.460
resprouting	148.784	-0.418	5.421	0.083	-0.125	0.528	0.007	-0.464	7.786	0.102

## Semiciduous forest

The chi-square of independence between the two variables is equal to 709.8971 (p-value = 1).

Eigenvalues	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9	
Variance	0.224	0.194	0.177	0.162	0.129	0.117	0.069	0.063	0.028	
%ofvar.	19.266	16.680	15.226	13.952	11.074	10.029	5.925	5.443	2.406	
Cumulative%ofvar.	19.266	35.946	51.172	65.123	76.197	86.226	92.151	97.594	100.000	
Rows(the 10 first)	Iner*1000	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
Astronium_fraxinifolium	12.199	0.154	0.087	0.016	-0.426	0.767	0.122	0.312	0.449	0.065
Astronium_graveolens	9.512	-0.207	0.125	0.029	-0.744	1.868	0.381	0.605	1.354	0.252
Spondias_mombin	3.496	-0.229	0.153	0.098	-0.216	0.157	0.087	0.046	0.008	0.004
Tapirira_guianensis	6.426	-0.604	0.801	0.279	0.597	0.904	0.273	-0.083	0.019	0.005
Annona_sylvatica	10.927	0.581	1.481	0.303	-0.052	0.014	0.002	-0.340	0.642	0.104
Unonopsis_guatterioides	11.835	0.352	0.453	0.086	0.003	0.000	0.000	-0.597	1.650	0.247
Xylopia_aromatica	9.728	0.502	1.288	0.296	0.067	0.026	0.005	-0.590	2.257	0.411
Aspidosperma_pyrifolium	5.008	-0.061	0.008	0.004	-0.514	0.670	0.259	0.064	0.011	0.004
Hancornia_speciosa	13.371	0.560	1.145	0.192	-0.084	0.030	0.004	-0.960	4.267	0.565
Tabernaemontana_catharinensis	4.587	-0.415	0.503	0.245	0.350	0.414	0.175	-0.133	0.066	0.025
Columns	Iner*1000	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
Hmax	96.024	-0.128	1.014	0.024	-0.462	15.350	0.310	0.185	2.677	0.049
SSD	156.067	-0.305	1.976	0.028	-0.630	9.734	0.121	0.937	23.544	0.267
phenology	109.760	-0.479	10.396	0.212	0.534	14.918	0.263	-0.116	0.773	0.012
leaf_cha	147.618	0.817	19.989	0.303	-0.143	0.709	0.009	0.398	5.997	0.072
Spinescence	184.476	1.880	23.247	0.282	2.283	39.610	0.416	1.466	17.892	0.172
Flower_size	162.273	1.618	34.434	0.475	-0.610	5.656	0.068	-1.032	17.742	0.193
Flower_color	63.427	0.073	0.371	0.013	-0.172	2.379	0.073	-0.120	1.260	0.035
pollination	28.671	-0.031	0.096	0.008	-0.044	0.224	0.015	0.016	0.032	0.002
dispersal_syn	74.093	-0.347	8.471	0.256	0.299	7.269	0.190	-0.004	0.001	0.000
resprouting	139.452	0.012	0.004	0.000	0.342	4.151	0.058	-0.880	30.080	0.382

# Transitional forest

The **chi-square** of independence between the two variables is equal to **408.6947** (p-value = 1).

Eigenvalues	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	Dim.9	
Variance	0.243	0.198	0.154	0.137	0.131	0.101	0.065	0.056	0.027	
%ofvar.	21.868	17.797	13.896	12.295	11.793	9.096	5.852	5.015	2.387	
Cumulative%ofvar.	21.868	39.665	53.561	65.856	77.649	86.745	92.597	97.613	100.000	
Rows(the10first)	Iner*1000	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
Astronium_fraxinifolium	20.409	-0.151	0.128	0.015	0.550	2.077	0.201	-0.001	0.000	0.000
Tapirira_guianensis	11.042	0.553	1.028	0.226	-0.674	1.875	0.336	0.155	0.126	0.018
Annona_montana	15.605	-0.300	0.505	0.079	-0.151	0.156	0.020	0.361	1.145	0.113
Xylopia_aromatica	12.544	-0.465	1.692	0.327	0.043	0.018	0.003	0.511	3.222	0.396
Aspidosperma_australe	15.011	-0.504	0.854	0.138	0.094	0.037	0.005	-0.962	4.890	0.503
Aspidosperma_cylindrocarpon	9.549	-0.180	0.109	0.028	-0.265	0.289	0.060	-0.575	1.749	0.283
Himatanthus_obovatus	15.502	-0.266	0.237	0.037	-0.076	0.024	0.003	0.884	4.129	0.411
Dendropanax_cuneatus	9.479	0.388	0.675	0.173	-0.651	2.331	0.486	-0.294	0.611	0.099
Acrocomia_aculeata	30.840	0.851	4.860	0.383	0.384	1.214	0.078	0.534	3.014	0.151
Attalea_phalerata	7.764	0.311	0.433	0.135	-0.507	1.413	0.360	0.166	0.193	0.038

Transitional forest										
Columns	Iner*1000	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
Hmax	115.263	-0.053	0.130	0.003	-0.258	3.854	0.066	-0.645	30.750	0.412
SSD	135.807	0.551	5.785	0.103	1.103	28.460	0.414	0.056	0.094	0.001
phenology	112.136	0.508	10.095	0.219	-0.579	16.140	0.284	0.294	5.335	0.073
leaf_cha	130.224	-0.684	15.714	0.293	0.477	9.367	0.142	-0.378	7.537	0.089
Spinescence	171.394	2.081	29.084	0.412	1.932	30.780	0.355	-0.077	0.062	0.001
Flower_size	157.280	-1.353	28.696	0.443	0.566	6.168	0.078	0.448	4.951	0.049
Flower_color	56.119	-0.205	2.779	0.120	-0.002	0.000	0.000	0.078	0.632	0.017
pollination	26.643	-0.009	0.007	0.001	-0.093	0.955	0.071	-0.111	1.769	0.102
dispersal_syn	76.738	0.319	6.853	0.217	-0.228	4.274	0.110	-0.001	0.000	0.000
resprouting	128.979	-0.179	0.857	0.016	-0.007	0.002	0.000	1.075	48.869	0.585

**SI1.** R code for (I) Generating phylogenetic trees using V.PhyloMaker2, (II) Calculating the D statistic for the phylogenetic structure of a binary variable, (III) Visualizing the generated phylogenetic trees, (IV) Creating Parallel Coordinates Visualization, and (V) Performing Correspondence Analysis and Visualization.

# I. Generating phylogenetic trees using V.PhyloMaker2

library("V.PhyloMaker2")

example <- read.csv("species\_list.csv")</pre>

tree <- phylo.maker(sp.list = example, tree = GBOTB.extended.TPL, nodes = nodes.info.1.TPL, scenarios = "S3")

write.tree(tree\$scenario.3, "sample.tre")

#### II. Calculation of D statistic for the phylogenetic structure of a binary variable

library(caper) library(phytools) library(vegan) library(geiger)

tree <- read.tree("tree") plot(tree, cex=0.4) tree\$node.label <- NULL

traits <- read.csv("traits.csv")
head(traits)</pre>

spdata <- comparative.data(tree, traits, "species")</pre>

spdata2 <- na.omit(spdata)</pre>

variable <- spdata2\$variable
PhyloD <- phylo.d(spdata2, binvar=variable)
print(PhyloD) # Display the calculated D statistic</pre>

plot(PhyloD)

# III. Generating the visualization of the generated phylogenetic trees

library(ggplot2) library(ggtree) library(cowplot) library(gridExtra) library(grid)

```
tree1 <- read.tree("arvore_decidual")</pre>
tree2 <- read.tree("arvore_semidecidual")</pre>
tree3 <- read.tree("arvore_transição")</pre>
color_palette <- c("#F67280", "#FFA07A", "#8FBBAF", "#6B7B8E")
title1 <- expression("A. Deciduous forest")
title2 <- expression("B. Semideciduous forest")
title3 <- expression("C. Transitional forest")
layer1 <- ggtree(tree2, layout = "circular") +</pre>
 geom_tree(aes(color = branch)) +
 ggtitle(title1) +
 scale_colour_gradientn(colours = color_palette)
layer2 <- ggtree(tree2, layout = "circular") +
 geom_tree(aes(color = branch)) +
 ggtitle(title2) +
 scale_colour_gradientn(colours = color_palette)
layer3 <- ggtree(tree3, layout = "circular") +</pre>
 geom_tree(aes(color = branch)) +
 ggtitle(title3) +
 scale_colour_gradientn(colours = color_palette)
plot <- arrangeGrob(</pre>
 arrangeGrob(layer1, layer2, ncol = 2),
 arrangeGrob(layer3, ncol = 1),
 ncol = 1)
grid.draw(plot)
IV. Parallel Coordinates Visualization
library(ggplot2)
library(GGally)
library(readr)
my_palette <- c("#8FBBAF", "#6B7B8E", "#F67280")
data <- read_csv("phylo.d.csv")
ggparcoord(data = data,
      columns = 2:11,
      alphaLines = 0.9,
      groupColumn = "Forest",
      showPoints = TRUE,
      scale = "globalminmax") +
 theme(axis.text.x= element_text(angle = 30, vjust = 1))+
 scale_color_manual(values = my_palette) +
 geom_point(size = 2) +
 scale_y_continuous(limits = c(-1, 3)) +
 labs(x = "Traits", y = "D-values") +
 ggtitle("Estimated D values")
V. Correspondence Analysis and Visualization
```

library(vegan) library(FactoMineR) library(factoextra) library(ggplot2) library(gridExtra)

```
create_plot <- function(my_ca, title) {</pre>
 plot.CA(my_ca, selectCol = 'contrib 15', selectRow = 'contrib 99',
      unselect = 0, cex = 1.1, cex.main = 1.1, cex.axis = 1.1, habillage = 'contrib',
      col.col = '#0D00FF', invisible = c('row')) +
  theme(legend.position = "bottom") +
  scale_x_continuous(limits = c(-3, 3)) +
  scale y continuous(limits = c(-2, 3)) +
  scale_color_gradientn(colors = c("#8FBBAF", "#6B7B8E", "#FFA07A", "#F67280")) +
  labs(title = title, fill = "contrib")
}
data1 <- na.omit(read.csv("traits_decidual.csv", header = TRUE, row.names = 1))
data2 <- na.omit(read.csv("traits_semidecidual.csv", header = TRUE, row.names = 1))
data3 <- na.omit(read.csv("traits_transicao.csv", header = TRUE, row.names = 1))
my_ca <- lapply(list(data1, data2, data3), CA)
titles <- c(expression("A. Deciduous forest"),
       expression("B. Semideciduous forest"),
       expression("C. Transitional forest"))
plots <- lapply(1:3, function(i) create_plot(my_ca[[i]], titles[i]))</pre>
grid.arrange(grobs = plots, ncol = 3)
create species plot <- function(my ca, title) {</pre>
 plot.CA(my_ca, selectCol = 'contrib 15', selectRow = 'contrib 0',
      unselect = 0, cex = 1.1, cex.main = 1.1, cex.axis = 1.1, habillage = 'contrib',
      col.col = '#0D00FF') +
  theme(legend.position = "bottom") +
  scale_x_continuous(limits = c(-3, 3)) +
  scale_y_continuous(limits = c(-2, 3)) +
  scale_color_gradientn(colors = c("#8FBBAF", "#6B7B8E", "#FFA07A", "#F67280")) +
  labs(title = title, fill = "contrib")
}
species_plots <- lapply(1:3, function(i) create_species_plot(my_ca[[i]], titles[i]))</pre>
```

```
grid.arrange(grobs = species_plots, ncol = 3)
```

lapply(my\_ca, summary)

# **Chapter 2**

# Woody Plant Functional Traits and Environmental Drivers of Community Structure in Brazilian's Seasonal Forests

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#### **Funding information**

Brazilian Coordination for the Improvement of Higher Education Personnel (CAPES)

# ABSTRACT

1. This study identifies the primary functional traits of woody flora in the Seasonal Forests of Mato Grosso do Sul, Brazil, addressing the gap in understanding how these traits influence community structuring. We classified species into functional clusters based on their traits, analyzed the relationships among these clusters in a multivariate space, and examined their spatial distribution in relation to climate, pedology, and geomorphology. These insights are crucial for informing effective conservation and restoration strategies in these forests.

2. Reproductive and floral traits were crucial in the differentiation and spatial distribution of functional clusters. Characteristics like floral symmetry, size, and color impact floral production cost and the attraction of pollinators, which in turn influences reproductive success.

3. Dispersal syndromes and adaptive fruit characteristics were fundamental in the formation of species clusters. The morphological properties of fruits influence dispersal mechanisms and interactions with dispersal agents. Dispersal methods, such as wind and animal dispersal, shape the spatial structure and diversity of plant communities.

4. The spatial distribution of functional clusters across the phytogeographic domain reveals a flexible adaptation of plant species to diverse environmental conditions. However, preferences for specific topographic environments, soil types, and climate categories are evident. Environmental factors, particularly climate, significantly influence the distribution of functional clusters.

5. *Synthesis and applications.* Our findings highlight the significant role of reproductive and floral characteristics in the differentiation and spatial distribution of functional clusters. Additionally, they underscore the importance of understanding the complex relationships between functional traits and environmental factors for effective conservation and management strategies. Promoting resilience and functional heterogeneity through species integration and considering critical environmental factors can increase ecological resilience, stability, and diversity, contributing to the development of restoration and maintenance practices for biodiversity in impacted ecosystems.

# **KEYWORDS**

functional clusters, spatial distribution, environmental factors, reproductive traits, dispersal syndromes, ecological management, ecological resilience, biodiversity conservation

# Traços Funcionais de Plantas Lenhosas e Fatores Ambientais na Estrutura das Comunidades em Florestas Estacionais

#### Larissa Oliveira Vilela

# **RESUMO**

1. Este estudo identifica os principais traços funcionais da flora lenhosa nas Florestas Sazonais de Mato Grosso do Sul, Brasil, abordando a lacuna na compreensão de como esses traços influenciam a estruturação das comunidades. Classificamos as espécies em clusters funcionais com base em seus traços, analisamos as relações entre esses clusters em um espaço multivariado e examinamos sua distribuição espacial em relação ao clima, pedologia e geomorfologia. Esses insights são cruciais para informar estratégias eficazes de conservação e restauração nessas florestas.

2. Traços reprodutivos e florais foram cruciais na diferenciação e distribuição espacial dos clusters funcionais. Características como simetria floral, tamanho e cor das flores impactam o custo da produção floral e a atração de polinizadores, o que, por sua vez, influencia o sucesso reprodutivo.

3. Síndromes de dispersão e características adaptativas dos frutos foram fundamentais na formação dos clusters de espécies. As propriedades morfológicas dos frutos influenciam os mecanismos de dispersão e as interações com os agentes dispersores. Métodos de dispersão, como dispersão pelo vento e por animais, moldam a estrutura espacial e a diversidade das comunidades vegetais.

4. A distribuição espacial dos clusters funcionais por meio do domínio fitogeográfico sugere uma adaptação flexível das espécies de plantas a diversas condições ambientais. No entanto, são evidentes preferências por ambientes topográficos específicos, tipos de solo e categorias climáticas. Fatores ambientais, particularmente o clima, influenciam significativamente a distribuição dos clusters funcionais.

5. *Síntese e aplicações.* Nossos achados destacam o papel significativo das características reprodutivas e florais na diferenciação e distribuição espacial dos clusters funcionais. Além disso, ressaltam a importância de compreender as relações complexas entre características funcionais e fatores ambientais para estratégias eficazes de conservação e manejo. Promover resiliência e heterogeneidade funcional através da integração de espécies e considerando fatores ambientais críticos pode aumentar a resiliência ecológica, estabilidade e diversidade, contribuindo para o desenvolvimento de práticas de restauração e manutenção da biodiversidade em ecossistemas impactados.

## **PALAVRAS-CHAVE**

clusters funcionais, distribuição espacial, fatores ambientais, traços reprodutivos, síndromes de dispersão, manejo ecológico, resiliência ecológica, conservação da biodiversidade

#### 1 Introduction

The Atlantic Forest is one of the most biodiverse and unique forest biomes on Earth (Marques et al., 2021; Mittermeier et al., 2004; Myers et al., 2000), being considered a biodiversity hotspot (Laurance, 2009). Over time, urbanization, industrialization, and the expansion of agricultural activities have significantly modified natural environments, leading to extensive fragmentation and habitat loss (da Fonseca, 1985; Joly et al., 2014), with forest cover now reduced to just 24.3% (MapBiomas Project, 2023). In recent years, Brazil has experienced a process of degradation of its environmental and social policies and institutions (Abessa et al., 2019; Ferrante & Fearnside, 2019; Oliveira & Araújo, 2020; Ruggiero et al., 2021), posing a significant risk to a historically threatened biome.

Large-scale global initiatives for restoration and reforestation have been promoted worldwide to partially reverse the processes and consequences involved (Chazdon & Brancalion, 2019; Rosa et al., 2021). The commitments made in recent years for the restoration of the Atlantic Forest are numerous, ranging from the Atlantic Forest Restoration Pact and the National Plan for Native Vegetation Recovery (Planaveg) to Brazil's nationally determined contribution to the Paris Climate Agreement and the United Nations Decade on Ecosystem Restoration (2021–2030). The science of restoration ecology and its applied practice of ecological restoration has been contributing to overcoming these challenges (Dobson et al., 1997; Nellemann et al., 2010; Perring et al., 2015; Suding et al., 2015). However, regrouping functional ecological communities after their degradation is challenging, and transforming commitments into restored landscapes requires planning (Brancalion & Holl, 2020; Holl & Brancalion, 2020).

A critical aspect of this planning involves understanding how the choice of species or groups of species can influence ecosystem structure and functioning. In this context, the approach based on functional traits emerges as a valuable strategy that can have lasting effects on plant communities and positive implications for restoration efforts. In general terms, "functional trait" can be defined as morphological, biochemical, physiological, structural, phenological, or behavioural characteristics significantly influencing establishment, survival, and reproduction. These traits are expressed in individual phenotypes and are considered relevant for organisms to respond to the environment and/or have effects on ecosystem properties (Díaz et al., 2013; Garnier et al., 2016; Reich et al., 2003; Violle et al., 2007). Ecosystem properties and community productivity depend on the functional traits of the species that compose them (Roscher et al., 2012). For this reason, functional traits are considered the best approach for the overall predictive understanding of communities and ecosystems (Adler et al., 2014), allowing the organisation of species or individuals into groups with similar functions or responses

# (Rosenfield & Müller, 2020).

From this perspective, grouping species or functional groups with similar and relevant functional traits provides an adaptable framework for local context and restoration objectives (Laughlin, 2014). It is worth noting, however, that species often belong to more than one functional group, performing various functions at different levels (de Bello et al., 2010; Diaz et al., 2007), and their traits may contribute independently or jointly to the ecosystem (Carlucci et al., 2020; Gamfeldt et al., 2008). Thus, multiple functional traits reflect the diversity of ecosystem functions (Cadotte et al., 2011; Tsujii et al., 2020). Furthermore, communities with different species compositions can exhibit similar functionality (Laughlin et al., 2017), while communities predominantly composed of functionally similar species may not be resilient to environmental disturbances (Laughlin et al., 2018).

In recent years, traits have been employed to comprehend even the global dynamics of vegetation (Scholze et al., 2006) and the rate of ecosystem processes (Díaz & Cabido, 2001; Eviner & Chapin III, 2003; Garnier et al., 2004; Lavorel & Garnier, 2002). Although global databases such as the TRY Plant Trait Database (Kattge et al., 2020) contain information on functional traits, current knowledge is predominantly limited to species from temperate regions (Carlucci et al., 2020; Hortal et al., 2015) and much of the essential information for a large number of native tropical species is still lacking (Aerts & Honnay, 2011), or is still insufficient. For the Atlantic Forest, information on functional traits is scarce, focusing on tree species with small geographical distributions and no economic value (Petisco-Souza et al., 2020). The absence of basic information hampers the restoration of originally megadiverse tropical communities (Carlucci et al., 2020), particularly considering that the success of restoration efforts relies on the availability of taxonomic, ecological, physiological, and functional trait information for these species.

Knowledge about functional traits is indispensable for conserving and restoring biodiversity (Carlucci et al., 2020). Here, we focus on the functional traits of woody species in Seasonal Forests, a type of vegetation characterised by seasonality (alternation of rainy and dry periods) and belonging to the Atlantic Forest phytogeographic domain (Marques et al., 2021). Our analysis will encompass species from Semideciduous Seasonal Forests, where 20% to 50% of the trees shed their leaves in winter, and Deciduous Seasonal Forests, where more than 50% of the trees are deciduous (Marques et al., 2021), as well as species from Transition Forests to Forested Savannah or Riparian Forests.

The main objective of this study is to identify the key functional traits of the woody flora in the Seasonal Forests of the Mato Grosso do Sul state. Additionally, we aim to (i) group species into clusters based on their functional traits; (ii) analyze the relationships and overlaps among these functional groups in a multivariate space; and (iii) investigate the spatial distribution of species within these functional groups in Mato Grosso do Sul, examining potential correlations with environmental factors such as climate, pedology, and geomorphology. We expect to comprehend the functional traits that drive the formation of each functional cluster, the variations of traits within clusters, and the potential relationships between the spatial distribution of these clusters and environmental factors. This analysis will enable us to discuss how effective management of these clusters can be integrated into ecological restoration programs, with the goal of enhancing resilience and functional diversity in degraded areas.

# 2 Material and methods

#### 2.1 Species list

To gather information on the functional traits of woody plant species in Seasonal Forests, data were compiled from 470 species, including trees, shrubs, cacti, and palms, listed by Damasceno-Junior et al. (2018) for the state of Mato Grosso do Sul. To classify the species, we utilised occurrence records provided by Damasceno-Junior et al. (2018), and we grouped the plants into three distinct phytophysiognomies: Deciduous Seasonal Forest, Semideciduous Seasonal Forest, and Transition to Forested Savannah or Riparian Forests, referred to here as Transition Forest. Families were organised according to the Angiosperm Phylogeny Group (APG IV, 2016). Additionally, botanical nomenclature was standardised according to the Flora e Funga do Brasil (2023) <floradobrasil.jbrj.gov.br>

# **2.2 Plant Functional Traits**

We gathered information on the functional traits of species, which are related to essential aspects of their biology and ecology, and assigned presence and absence values to each trait (see Table 1). For this selection, we relied on previous studies (Fitter & Peat, 1994; Valladares et al., 2008), which were simplified to avoid ambiguities and overlapping concepts and definitions. The classification of wood density (SSD) followed the proposal by Jankowsky (1990) (Table 1). Regarding fruits, their classification regarding type, dehiscence, and adaptations for dispersal was mainly based on Barroso et al. (1999), which addresses the morphology of diaspores at the genus level, as well as the simplification of their work performed by Kuhlmann & Ribeiro (2016), also present in Kuhlmann & Fagg (2018a, 2018b) (Table S1). Regarding seed size, we used five qualitative categories according to Tabarelli & Peres (2002) and de Melo et al. (2006) (Table 1). The values of adult plant size (Hmax) were classified according to Stovall et al. (2019). Attributes related to plant survival, such as the ability to resprout and nitrogen fixation capacity, were also considered in this study.

# Table 1. Definition of traits and groups of traits used in the study

Characteristi	cs related to spatial occupation	Flavor calava	brown groonish			
Plant growth form	subshrub shrub tree palm	Flower colour	white or coloured			
Size of adult plant (Hmax)	small (height < 15m) medium (15m - 30m) large (height > 30 m)	Fruit dehiscence Fruit type	indehiscent dehiscent capsular follicular			
Plant phyllotaxis	alternate opposite		nucoid samaroid			
Stem epidermal characteristics	glabrous hispid lanate or very tomentose		bacold drupoid schizocarp arthrocarpal			
Whole plant sexuality	monoic dioic hermaphrodite polygamous	Adaptation	fleshy adherent elaiosome aril			
Stem specific density (SSD) or wood density (g.cm-3)	light (density < 0,50 g.cm-3) moderately dense (0,51 g.cm-3 - 0,75 g.cm-3) dense woods (0,76 g.cm-3 - 0,95 g.cm-3) o very dense woods (density > 0,96 g.cm-3)		pseudofruit resin mimetic seed plume			
Characterist	ics related to foliar morphology		winged light seeds			
Vegetative phenology	evergreen semi-deciduous deciduous	Seed size	explosive dehiscence very small (< 1 to 3 mm in length) or small (3.1 to 6 mm)			
Leaf compoundness	simple compound		medium (6.1 to 15 mm) large (15.1 to 30 mm) or very large (>30 mm in length)			
Leaf epidermal characteristics	glabrous hispid lanate or very tomentose	Dispersal syndrome	anemochorous autochorous			
Spinescence	absence presence	Dispersal agent	zoochorous wind mammaliochory			
Characteristics relat	ted to reproduction and seed dispersal		ornithochory			
Type of inflorescence	cymose racemose		myrmecochory chiropterochory mixed			
Flower symmetry type (flower shape)	actinomorphic zygomorphic	Surviva	I and nutrient-related traits			
Flower size	small (corolla < 5 mm) intermediate (5 mm - 20 mm) big (corolla > 20 mm)	Plant nitrogen (N) fixation capacity Plant resprouting capacity	absence presence absence presence			

## 2.3 Plant Functional Traits Database and species occurrence data

We obtained data on the functional traits (Table S2) from two databases: TRY - Plant Trait Database <try-db.org> (Kattge et al., 2020), global repository of plant characteristics, and BIEN -Botanical Information and Ecology Network database <bien.nceas.ucsb.edu/bien> through the R-package "R BIEN" (Maitner et al., 2018) in the statistical software R version 4.1.1 (R Core Team, 2021), using the RStudio Team environment (2022). Subsequently, we eliminated duplicate functional traits and outliers and calculated mean values, when necessary, for each species concerning the functional attribute. To complement the information on morphological characteristics and obtain data on species occurrence, we utilised two data sources: CRIA - Centro de Referência em Informação Ambiental <cria.org.br> and GBIF - Global Biodiversity Information Facility <gbif.org>. To access this information, we utilised the "rspecieslink" and "rgbif2" functions available in the R-package "plantR" (Lima et al., 2021) n the R statistical program. Next, we searched the literature (Table S3) for information on species that did not have attribute data in the abovementioned databases. Species without trait information were excluded from the analysis.

#### 2.4 Clustering analysis and pattern identification

To identify patterns in the data and group species into different clusters based on their characteristics, we conducted a clustering analysis using the functional traits data of the Seasonal Forest species. Firstly, the data were preprocessed by excluding rows with missing values using the "na.omit" function and normalised using the "scale" function, transforming each variable into a mean of zero and a standard deviation of one. The clustering analysis was performed using the R-package "stats" by employing the "kmeans" function, which divides the species into groups based on their similarities. To determine the number of groups, we utilised the R-package "factoextra" (Kassambara & Mundt, 2020) with the "fviz\_nbclust" function using the gap statistic method. A hierarchical clustering analysis was conducted using the "hcut" function, which generates a dendrogram illustrating the similarity relationships among the species. To extract the species list for each group, we used the group identification vector obtained from the "cutree" function and applied an anonymous function using "lapply" to obtain the species list for each group. Lastly, Principal Component Analysis (PCA) was performed using the R-package "stats" with the "prcomp" function, which reduces the dimensionality of the data and generates principal components that explain most of the data variance. PCA was carried out by phytophysiognomy to comprehend which variables had the greatest influence on cluster formation. All analyses were conducted in the statistical software R version 4.1.1 (R Core Team, 2021) within the RStudio Team environment (2022).

# 2.5 Geoprocessing and environmental data

To assess the spatial distribution of species composing the functional clusters across the Mato Grosso do Sul state, geoprocessing tools were employed to identify potential species distribution patterns concerning environmental factors. Utilising QGIS 3.30 software <qgis.org>, thematic maps were constructed incorporating geomorphological information (Figure S2), pedology data (Figure S3), and climate data (Figure S4) sourced from the Instituto Brasileiro de Geografia e Estatística (IBGE) <ibge.gov.br>. Occurrence data for the species obtained from CRIA and GBIF were exported and preprocessed to remove unnecessary information. In QGIS, this file was configured as a shapefile with a standardised coordinate reference system set to SIRGAS 2000 UTM Zone 18S. Geomorphological, pedology, and climate information were obtained from the Geosciences division of IBGE. Shapefile format data for these variables were acquired from IBGE and imported into QGIS. As these data covered the entire national territory, the GIS software's clipping tool was used to clip the layers and enhance the visibility of the study area. Attribute table information for each layer was saved, processed within QGIS, and utilised to verify correlations between clusters and environmental factors.

# 2.6 Data analysis

To identify patterns and trends in the data concerning different clusters and environmental variables, we employed the "ggparcoord" function from the R-package "GGally" (Schloerke et al., 2018) to generate parallel coordinate plots. To identify patterns of relationship and correlation among the data matrices, we utilised Multiple Factor Analysis (MFA) using the R-package "FactoMineR" (Lê et al., 2008). MFA is a multivariate technique based on the generalisation of Principal Component Analysis (PCA) aimed at analysing multiple sets of variable data collected on the same set of observations, providing a set of standard factorial scores and projecting each of the original data set to analyse communities and discrepancies (Abdi et al., 2013). MFA employs a factor analysis applied to the entire set of variables, where each group of variables is weighted, resulting in a canonical analysis (Escofier & Pages, 1994).

## **3** Results

# 3.1 Cluster analysis and general characterisation of resulting clusters

The optimal number of clusters established using the *gap statistic* technique for the Deciduous Seasonal Forest was determined as 2; for Semideciduous Seasonal Forest, it was determined as 4; and for Transition Forest, it was determined as 3 (Figure S1). The partitioning clustering plot identified the clusters for the three physiognomies (Figure 1).



**Figure 1.** Partitioning clustering plot showing the identified clusters of three seasonal forest phytophysiognomies using k-means clustering. The points on the plot represent plant samples, and their colours indicate which cluster each sample belongs to.

In Deciduous Forests, there is a significant differentiation among the clusters (Figure 1). The traits that contributed the most to the variance and formation of the clusters were related to fruit characteristics, flower characteristics, leaf characteristics, and seed dispersal (Figure 2). Cluster 1 (DC1) is

mainly characterised by plants with indehiscent fruits, fleshy berries, or a fleshy aril surrounding the seeds, strongly associated with zoochoric dispersal by ornithochory and mammaliochory. These plants have simple leaves and glabrous stems, with actinomorphic flowers that are small and green. Cluster 2 (DC2), on the other hand, is primarily characterised by plants with dehiscent fruits, follicular and capsular, with the presence of winged expansions associated with anemochory. Plants in DC2 have compound leaves and white or colourful zygomorphic flowers.



**Figure 2.** PCA biplot showing the main variables that explain the most variance in data grouped by each type of Seasonal Forest. The points represent the species, and the arrows indicate the variables' contribution to each cluster's formation. The elliptical areas highlight the high-density regions in each cluster.

The results indicated the presence of four distinct clusters (Figure 1) in the Semideciduous Forests. Cluster 3 (SC3) exhibits relationships with the other three clusters, particularly with Clusters 1 (SC1) and 4 (SC4), which also show overlaps between them and are distributed across the biplot dimensions primarily due to leaf composition. Cluster 2 (SC2) differs from the others, being more distant and sharing characteristics solely with SC3. The traits that contributed the most to the variance and formation of the clusters are related to reproductive aspects, involving fruits, their adaptations, and lispersal syndrome, as well as traits associated with flowers and epidermal characteristics of stems and leaves. SC1 is primarily characterised by small, evergreen plants with simple leaves, fleshy bacoid fruits, zoochorous dispersal, cymose inflorescences, and actinomorphic flowers. SC2 stands out from the other clusters by featuring plants with wing-like expansions associated with anemochory and zygomorphic flowers. The SC3 group shares characteristics with all clusters and is more heterogeneous regarding functional traits. This group consists of plants with simple leaves, tomentose stems and leaves, and plants with compound leaves, glabrous stems and leaves, racemose as well as cymose inflorescences, and arcupoid fruits. Lastly, SC4 shares characteristics with SC1 and SC3 and primarily comprises small-flowered palms with glabrous leaves.

The Transition Forests were divided into three different clusters (Figure 1). Cluster 1 (TC1) exhibits similarities and shares attributes with Cluster 2 (TC2) but primarily with Cluster 3 (TC3). There are no characteristic similarities between the latter two. The variance and formation of the clusters were also related to reproduction-oriented attributes, such as fruit characteristics, adaptations, and seed dispersal. The first group, TC1, comprises medium-height species with compound and alternate leaves, small flowers, and adaptations involving fleshy and colourful arils surrounding the seeds. TC2, on the other hand, groups species with adaptations of wing-like expansions associated with anemochorous dispersal, dehiscent and capsular fruits, and flowers with zygomorphic symmetry. Finally, TC3 is represented by small plants with indehiscent, bacoid, and drupoid fruits, fleshy and associated with zoochorous dispersal. Additionally, the presence of species with small and actinomorphic flowers is observed.

# 3.2 Spatial distribution of clusters in the phytogeographic domain and their relationship with environmental factors

The analysis of the spatial distribution of species within functional clusters across the phytogeographic domain and the state of Mato Grosso do Sul revealed distinct patterns. Each cluster's predominant areas and zones of overlap were identified, highlighting the spatial organization of these clusters. In various proportions, the clusters exhibited remarkably similar distribution patterns across different categories of geomorphology, pedology, and climatic types (Figure 3). The clusters were predominantly distributed in regions characterised by Latossolo and Neossolo, primarily in Hills, Plains,

and Depressions, with a hot and humid climate accompanied by 1 to 2 or 3 dry months or a sub-hot humid climate with 1 to 2 dry months.



**Figure 3.** Distribution of clusters among the A. Geomorphology, B. Climate type and C. Pedology classes. In the geomorphology class, "Dep" represents Depressions, "High" represents Highlands, "Hill" represents Hills, "Plan" represents Plains, and "Plateau" represents Plateaus. In the climate type class, "Hot1-2" corresponds to Hot, humid (1 to 2 dm), "Hot3" corresponds to Hot, humid (3 dm), "Hot4-5" corresponds to Hot, semi-humid (4 to 5 dm), "SubHot1-2" corresponds to Sub-hot, humid (1 to 2 dm), and "SubHot3" corresponds to Sub-hot, humid (3 dm). Finally, in the pedology class, "Argi" stands for Argissolo, "Camb" stands for Cambissolo, "Cher" stands for Chernossolo, "Gleis" stands for Gleissolo, "Latos" stands for Planossolo, and "Plinto" stands for Plintossolo.

Although there are similarities in the distribution of species belonging to the clusters across environmental factors, significant differences influence the distribution of plant species. The Multiple Factor Analysis (MFA) based on geomorphology, pedology, and climate type data indicates that these factors strongly influence the clusters. Dim.1 explained the majority of the total variability (81.1%), followed by Dim.2 (7.0%) and Dim.3 (5.7%). The cumulative sum of eigenvalues shows that the first three dimensions explained 93.9% of the total variability. Geomorphology, pedology, and climate type exhibit high loadings on the first component (Dim.1), while the most significant loadings of the second component (Dim.2) are observed in pedology and climate (Figure S2, S3, and S4).

All variables have a strong positive correlation structure, demonstrating that they are highly interconnected (Table S5). The variables related to geomorphology and climate had a more significant contribution to the results of the MFA than the other variables associated with pedology (Figure 4b). Clusters TC1, TC2, and SC4, as well as DC2 and TC3, grouped in regions of the graph (Figure 4a), for example, exhibit more similar profiles concerning the considered variables than the remaining clusters.



**Figure 4.** Multiple Factor Analysis (MFA): A. Individual factor map where points represent the centroid of clusters concerning Principal Component Analyses (PCA) of each group of variables. The colours used indicate different groups of variables, and the distance between the points represents their similarity or dissimilarity; B. Global PCA presents the correlation among multiple variables. The colours used indicate the contribution of each variable to the analysis, and the position of the points on the graph indicates the relationship between them.

Considering that the proximity of the points to the arrows indicates the contribution of these variables to the observed differences between groups, the observed patterns of association between environmental characteristics and the clusters suggest that each forest type presents a specific dynamic. The closer the point is to the arrow, the stronger the association between the variable and the respective cluster. Therefore, it is possible to observe that the different groups of variables have distinct strengths of influence among the different clusters.

# 4 Discussion

Although reproduction is one of the key aspects of individuals' fitness, reproductive and floral traits have played a secondary role in the ecology of functional traits and trait-based community assembly studies (E-Vojtkó et al., 2020). Nonetheless, the findings here reinforce the importance of traits

associated with seed reproduction and dispersal in functional clusters' differentiation and spatial distribution. Floral characteristics, which play a crucial role in attracting pollinators and seed production (Faegri & Pijl, 1979), were particularly significant for the differentiation of clusters, especially in the species and physiognomies observed in this study. Floral symmetry, for instance, has been considered a determining factor in pollination syndromes (Ashworth et al., 2015; Rosas-Guerrero et al., 2014; Yoder et al., 2020). Additionally, flower size and colour directly affect the cost of flower production and, consequently, their ability to attract pollinators (E-Vojtkó et al., 2022; Krizek & Anderson, 2013).

Although in some species or habitats the relationship between fitness and floral traits may appear subtle, typically during the sexual reproduction phase of the plant life cycle, floral traits assume great importance for maximising reproductive success (Larson & Funk, 2016). This significance is partially attributed to the fact that larger flowers generally contain more nectar and are more visible to pollinators (Blarer et al., 2002; Fenster et al., 2006), have been associated with phenotypic selection for larger flowers (Zhao et al., 2020), and that flower colour components can serve as signalling cues for pollinators (Garcia et al., 2014; Horth et al., 2014; Lunau, 2000; Trunschke et al., 2021; Van Der Kooi et al., 2021; Verhoeven et al., 2018), which may increase visitation rates (Fenster et al., 2006; Krizek & Anderson, 2013) and, consequently, the probability of fertilisation.

The dispersal syndrome and fruits' adaptive characteristics played a crucial role in clustering species in all cases. These characteristics are closely related, as the morphological properties of fruits influence how they are dispersed and act as a selective barrier that restricts interaction with seed dispersal agents at the community level (Bender et al., 2018; Burns, 2013; Dehling et al., 2016; Olesen et al., 2011; Rojas et al., 2022). Dispersal is the only means by which plants can colonize new habitats; hence it is understandable that plants have evolved various physical methods to accomplish this task (Seale & Nakayama, 2020), being a fundamental process that shapes the spatial structure and diversity of plant communities (Morán-López et al., 2018). The distances over which seeds are dispersed are critical for examining the spatial patterns of seed dispersal and their implications for plant reproductive success and population structure.

Plants with large seeds and fruits featuring attractive adaptations for fauna, for instance, rely on animals for their dispersal, whereas those with lighter and smaller seeds, along with adaptations such as wing-like expansions or plumes, are more easily dispersed by wind over long distances (Ghamari et al., 2010; Pijl, 1982; van Rheede van Oudtshoorn & van Rooyen, 1999). In tropical regions, where a significant portion of plants relies on vertebrates for seed dispersal, frugivores play a vital role in shaping plant communities, and their behavior can influence the spatial distribution of dispersed seeds and

accelerate succession in planted stands compared to natural succession (De La Peña-Domene et al., 2014; Gopal et al., 2020).

The similarities in fruit characteristics have originated through complex evolutionary pathways in response to mutualistic interactions with dispersers - Dispersal Syndrome Hypothesis (DSH; Valenta & Nevo, 2020), and currently, they influence the interaction between species and dispersers (Blendinger et al., 2016; Dehling et al., 2016; González-Castro et al., 2015). The contributions of dispersal syndromes, fruit adaptations, and flower characteristics in shaping different clusters indicate that the plants of the phytophysiognomies in question have evolved to exploit different ecological niches in the region and underscore the importance of these traits in the structuring of these communities.

The DC2, SC2, and TC1 clusters, predominantly composed of anemochorous species, share characteristics such as wing expansions and zygomorphic flowers. In DC2 and TC1, the fruits are predominantly capsule-shaped, while in SC2 they are mostly samaroid. Anemochory, or wind dispersal, is highly frequent, particularly in drier and more open environments (Jara-Guerrero et al., 2011; Soons et al., 2004). Fruit modifications such as wing expansions primarily serve to enhance the diaspore's resistance to air, thus prolonging its flight time and expanding its capacity for wind-mediated transport (Eriksson & Kainulainen, 2011; Minami & Azuma, 2003; van Rheede van Oudtshoorn & van Rooyen, 1999; Zhang et al., 2014). The wings found in species belonging to clusters of anemochorous species aid in gliding when symmetrically arranged, and when arranged asymmetrically, they provide dynamic propulsion. This is why most tree species with winged diaspores are large (Minami & Azuma, 2003; van Rheede van Oudtshoorn & van Rooyen, 1999).

The remaining clusters, mostly composed of zoochorous species, also share characteristics such as small, actinomorphic flowers and mainly bacoid or drupoid fruits, fleshy or with fleshy aril surrounding the seeds. Zoochory is a phenomenon associated with forest environments, owing to the high diversity of frugivorous species in these habitats (Willson et al., 1990). To attract the dispersing species, properties such as colour, odour, and size play a determining role (Fahn & Werker, 1972). Adaptations such as the presence of fleshy and colourful aril surrounding the seeds and fleshy fruits fulfil the role of making the diaspore more attractive to fauna, particularly avian and mammalian frugivores (Evrard et al., 2019; Fleming & John Kress, 2011; Pijl, 1982; Skutch, 1980; Valenta & Nevo, 2020).

Regarding floral symmetry, zygomorphic flowers are associated with higher rates of diversification (O'Meara et al., 2016; Sargent, 2004; Vamosi & Vamosi, 2010) and are commonly considered more specialised than those with actinomorphic symmetry, which is regarded as an axiom of pollination ecology (Darwin, 1877; Endress, 2012; Stebbins, 1974; Takhtajan, 1981). Actinomorphic flowers, with their radial symmetry, are often associated with generalist pollinators due to easy access to

nectar and pollen from all directions, attracting a wide range of pollinators, including bees, butterflies, and beetles, whereas zygomorphic flowers are typically specialized for pollination by specific pollinator species (Chapman et al., 2012; Lázaro et al., 2008). However, at both the global and community levels, plants with zygomorphic flowers tend to have fewer visitor species and, therefore, may be more susceptible to pollinator loss (Yoder et al., 2020).

The spatial distribution pattern of functional clusters throughout the phytogeographic domain in the state of Mato Grosso do Sul significantly contributes to understanding the determinants of the relationship between the floristic composition of these areas and various environmental factors. The presence of clusters in distinct geomorphological, pedological, and climatic categories (Figure 3) suggests a flexible adaptation of plant species to diverse environmental conditions. However, a preference for specific topographic environments (Plains, Hills, and Depressions), soil types (Latossolo and Neossolo regions), and climate types (hot and humid with 1 to 2 or 3 dry months, or sub-hot with 1 to 2 dry months) is evident. Despite this, the MFA indicated that these variables do not uniformly affect all clusters and that these groups of variables exert different levels of influence on each cluster. In most cases, climate was highly correlated with the clusters, serving as a crucial factor in determining their distribution.

The distribution and patterns of plant species are influenced by a multitude of environmental factors that interact to shape the composition and structure of plant communities. The influence of climate on plant species distribution has been extensively documented from early biogeographers (Humboldt & Bonpland, 1805) to contemporary ecologists (Bañares-de-Dios et al., 2022; Morueta-Holme & Svenning, 2018; Willig et al., 2003). Climate, particularly temperature and precipitation, is considered the primary factor controlling the distribution of plant species at a continental scale (Thompson et al., 2006) and influences the composition patterns of plant communities and species distribution in tropical communities (Bañares-de-Dios et al., 2022; Engelbrecht et al., 2007; Esquivel-Muelbert et al., 2017; Hawkins et al., 2003; Ter Steege et al., 2006; Woodward et al., 2004). Moreover, precipitation and temperature have been identified as significant drivers of the large-scale geographic distribution of species with fleshy fruits (Zhao et al., 2018). Understanding these dynamics is crucial for predicting how plant communities will respond to future environmental changes.

The distribution patterns of shrub and tree species are deeply influenced by climate, affecting the diversity, composition, and interactions of plant communities. Historical climatic conditions have a lasting influence on the distribution of shrubs and trees, highlighting the climate's impact on woody plant diversity (Loidi et al., 2021). Furthermore, both tree and shrub richness exhibit similar responses to climatic variables, indicating large-scale spatial autocorrelation patterns in response to climate (Speziale et al., 2010). Climate change poses a significant threat to ecosystems, altering species
distribution and composition patterns and modifying the dynamics of plant communities, leading to changes in vegetation structure and biodiversity (Limpens et al., 2021; Mod & Luoto, 2016). Understanding the intricate relationships between climate and woody plant species is crucial for effective conservation and management strategies in the face of ongoing environmental changes.

The results underscore the importance of functional traits related to reproduction and dispersal in categorizing and understanding species within their distinct ecological clusters. The notable overlap and significant interrelation among functional groups in different clusters suggest that these groups are not strictly isolated but rather parts of a complex ecological *continuum*. The spatial distribution of species, correlated with specific environmental factors observed in this study, reinforces the need for targeted management strategies in ecological restoration programs. Climate and geomorphology emerge as determining factors, while soil characteristics also play an important role in the pattern of species distribution.

Promoting resilience and functional heterogeneity in the restoration of Seasonal Forests can be achieved by integrating species based on specific functional traits associated with seed reproduction and dispersal, and by considering critical environmental factors related to these species. For the studied sample universe, it is recommended to focus on functional traits such as fruit shape and size, which can influence dispersal effectiveness, and flower morphology, which affects attractiveness to pollinators. This approach can enhance ecological resilience by reducing vulnerability to environmental changes and the loss of specific pollinators, while promoting stability and ecological diversity. These recommendations are crucial for developing more effective and sustainable restoration practices, contributing to the recovery and maintenance of biodiversity in impacted ecosystems.

#### **5** Acknowledgments

This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. We thank Dr. Fátima C. M. Piña-Rodrigues and Dr. Sandro M. Silva for their friendly suggestions and comments on early versions of the manuscript.

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# **Supporting Information**

**Table S1.** Characterisation of fruit types according to Barroso (1999), Kuhlmann & Ribeiro (2016), and Kuhlmann &Fagg (2018a, 2018b).

	Fruit type	Characteristics
1	Capsular	Dry, dehiscent fruits formed by two or more carpels.
2	Follicular	Dry, dehiscent fruits formed by only one carpel.
3	Nucoid	Dry, indehiscent fruit.
4	Samaroid	Dry, indehiscent, winged fruits.
5	Bacoid	Fleshy fruits without the formation of a pit surrounding the seeds.
6	Drupoid	Fleshy fruits with the formation of a pit surrounding the seeds.
7	Schizocarp	Dry, indehiscent fruits segregate into smaller dispersion units.
8	Arthrocarpal	Fruit dry, indehiscent, uni carpellate, segregated into smaller units.

## **Table S2.** Trait List and TraitID in the TRY database.

Trait_ID	Trait name
917	Fruit width (diameter)
2934	Inflorescence type
2935	Flower symmetry type (flower shape)
29	Pollination syndrome
2940	Fruit dehiscence type
99	Fruit type
27	Seed length
28	Dispersal syndrome
1251	Plant vegetative phenology (leaf phenology)
17	Leaf compoundness
8	Plant nitrogen(N) fixation capacity
819	Plant resprouting capacity
4	Stem specific density (SSD) or wood density (stem dry mass per stem fresh volume)
24	Bark thickness
14	Leaf nitrogen (N) content organic per leaf dry mass
15	Leaf phosphorus (P) content per leaf dry mass
3086	Leaf area per leaf dry mass (specific leaf area, SLA or 1/LMA) petiole, rhachis and midrib excluded
660	Leaf nitrogen (N) content organic per leaf dry mass
15	Leaf phosphorus (P) content per leaf dry mass
33	Leaf photosynthesis rate per leaf area
3086	Leaf area per leaf dry mass (specific leaf area, SLA or 1/LMA) petiole, rhachis and midrib excluded

Table S3. List of literature from which additional functional trait information was obtained.

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**Figure S1.** The optimal number of clusters for the three seasonal forest phytophysiognomies, determined using the *gap statistic* method.



Table S4: Species grouped by Cluster, with a focus on those for which occurrence data is not available.

#### **Cluster Species**

SC1	Allophylus_edulis	
SC1	Apuleia_leiocarpa	
SC1	Aspidosperma_pyrifolium	
SC1	Astronium_fraxinifolium	
SC1	Astronium_graveolens	unavailable data
SC1	Calycophyllum_multiflorum	
SC1	Cariniana_estrellensis	
SC1	Cedrela_fissilis	
SC1	Ceiba_speciosa	
SC1	Cordia_trichotoma	
SC1	Coutarea_hexandra	
SC1	Diplokeleba_floribunda	
SC1	Diptychandra_aurantiaca	
SC1	Gallesia_integrifolia	
SC1	Handroanthus_heptaphyllus	
SC1	Handroanthus_ochraceus	
SC1	Handroanthus serratifolius	
SC1	Kielmeyera coriacea	
SC1	Lafoensia pacari	
SC1	Luehea candicans	
SC1	Luehea grandiflora	
SC1	Luehea paniculata	
SC1	Machaerium stipitatum	
SC1	Machaerium villosum	
SC1	Peltophorum dubium	
SC1	Plathymenia reticulata	
SC1	Platypodium elegans	
SC1	Simira sampaioana	unavailable data
SC1	Sparattosperma leucanthum	
SC1	Spondias mombin	unavailable data
SC1	, Sweetia fruticosa	
SC1	Tabebuia aurea	
SC1	Tabebuja roseoalba	
SC1	Terminalia araentea	
SC1	Terminalia corruaata	
SC1	Terminalia alabrescens	
SC1	Trema micrantha	
SC1	Triplaris aardneriana	
SC2	Aeaiphila intearifolia	
SC2	Aaonandra brasiliensis	
SC2	Alovsia viraata	
SC2	Annona sylvatica	
SC2	Apeiba tibourbou	unavailable data
SC2	Blepharocalyx salicifolius	
SC2	Brosimum aqudichqudii	
202	gaaalenaaan	

#### **Cluster Species**

DC1	Coutarea_hexandra	
DC1	Diatenopteryx_sorbifolia	
DC1	Dilodendron_bipinnatum	
DC1	Dimorphandra_mollis	
DC1	Diplokeleba_floribunda	
DC1	Enterolobium_contortisiliquum	
DC1	Guibourtia_hymenaeifolia	
DC1	Handroanthus_impetiginosus	
DC1	Handroanthus_serratifolius	
DC1	Helietta_apiculata	
DC1	Hymenaea_martiana	
DC1	Lachesiodendron_viridiflorum	unavailable data
DC1	Luehea_divaricata	
DC1	Machaerium_acutifolium	
DC1	Magonia_pubescens	
DC1	Maprounea_brasiliensis	
DC1	Maprounea_guianensis	
DC1	Ormosia_arborea	
DC1	Peltophorum_dubium	
DC1	Pilocarpus_pennatifolius	
DC1	Pseudobombax_grandiflorum	
DC1	Pseudobombax_longiflorum	
DC1	Pterogyne_nitens	
DC1	Samanea_tubulosa	
DC1	Sapium_glandulosum	
DC1	Sapium_haematospermum	
DC1	Schinopsis_brasiliensis	unavailable data
DC1	Senegalia_polyphylla	
DC1	Senegalia_tenuifolia	
DC1	Senna_spectabilis	unavailable data
DC1	Sterculia_apetala	unavailable data
DC1	Sterculia_striata	
DC1	Strychnos_pseudoquina	
DC1	Tabebuia_roseoalba	
DC1	Terminalia_fagifolia	
DC1	Trichilia_catigua	
DC1	Triplaris_americana	unavailable data
DC1	Zanthoxylum_caribaeum	unavailable data
DC1	Zanthoxylum_fagara	unavailable data
DC1	Zanthoxylum_rhoifolium	unavailable data
DC1	Zeyheria_montana	
DC1	Zygia_latifolia	
DC2	Agonandra_brasiliensis	
DC2	Andira_cujabensis	
DC2	Annona_coriacea	

## **Cluster Species**

SC2	Cecropia pachystachya	
502	Cestrum schlechtendalii	
502		
SC2	Chrysophyllum_marginatum	
5C2	Cordia sellowiana	
662	Condiana accellia	
SC2	Coraiera_sessilis	
SC2	Dendropanax cuneatus	
662		
SCZ	Diaymopanax_morototoni	unavallable data
SC2	Dipteryx alata	
502	Fruthrowlum danhaitos	
SCZ	erythroxylum_aaphintes	
SC2	Eugenia pyriformis	
sc2	Eugenia subterminalis	
302	Lugeniu_subterninuns	
SC2	Garcinia brasiliensis	
502	Guanira onnosita	
302	Guupiiu_oppositu	
SC2	Guazuma_ulmifolia	unavailable data
5C2	Hancornia sneciosa	
502	nunconna_speciosa	
SC2	Holocalyx_balansae	
SC2	lacaratia spinosa	
662	Lastabalana annifalisa	
SC2	Leptobalanus_parvifollus	
SC2	Maclura tinctoria	
602		
SC2	Nielicoccus_lepidopetalus	
SC2	Mimosa bimucronata	
600	Muraia quianoncia	
SCZ	wyrcia_gulanensis	
SC2	Myrcianthes pungens	
600	Auroiaria topolla	
SCZ	wyrciana_tenena	
SC2	Myrsine quianensis	
502	Porcog willdonovii	
SCZ	Persea_willdenovii	
SC2	Piper amalago	
502	Poutoria torta	
302	Poulenu_lonu	
SC2	Priogymnanthus hasslerianus	
502	Prockia crucis	
302	PIOCKIU_CIUCIS	
SC2	Psidium_sartorianum	
502	Psychotria carthagenensis	
502	- sychotha_culthagenensis	
SC2	Randia_armata	
5C2	Rudaea iasminoides	
602		
SC2	Rudgea_viburnoides	
SC2	Simarouba amara	
662	Ciana a	
SC2	Siparuna_guianensis	
SC2	Sloanea auianensis	
600	Corocoa honnlandii	
SCZ	sorocea_bonpianan	
SC2	Styrax camporum	
\$C2	Talicia acculenta	
302	Tulisiu_esculetitu	
SC2	Tapirira_guianensis	unavailable data
502	Inononsis quatterioides	
502	ononopsis_guatteriolaes	
SC2	Urera_baccifera	unavailable data
5C2	Vitex cymosa	
662	Videnia and sting	
SC2	xyiopia_aromatica	
SC3	Albizia niopoides	
662	Alebawaan diasalaw	
363	AICHOMEQ_UISCOIDI	
SC3	Alchornea alandulosa	
\$(7)	Alchornea triplinervia	
303	Alchonneu_tripinierviu	
SC3	Anadenanthera peregrina	
503	Cabralea canierana	
505		
SC3	Casearia_obliqua	
SC3	Casearia sylvestris	
505	Canadiana la fil	
SC3	copaijera_langsdorffii	
SC3	Croton floribundus	
500	Croton unusure	
363	croton_urucurana	
SC3	Enterolobium contortisiliauum	
\$(7)	Enuthring mulungu	
363	Liyunna_mulungu	
SC3	Geoffroea spinosa	
503	Guarea auidonia	
505		
SC3	Guarea_kunthiana	
SC3	Guarea macrophvlla	
502	Cubourtia burganacitalia	

## **Cluster Species**

DC2	Annona_cornifolia	
DC2	Annona emarainata	
	Annona nutans	
	Campamanasia vanthasarna	
DCZ		
DC2	Celtis_iguanaea	
DC2	Celtis_spinosa	
DC2	Cestrum mariquitense	
DC2	Chrysonhyllum aonocarnum	
	Chrysonbyllum margingtum	
	Cinysophynum_murginutum	
DC2	Diospyros_inconstans	
DC2	Erythroxylum_cuneifolium	
DC2	Erythroxylum_pelleterianum	
DC2	Eugenia florida	
	Genina americana	
	Cuapira arealata	
DCZ		
DC2	Hieronyma_aicnorneolaes	
DC2	Maclura_tinctoria	
DC2	Myrcia_bella	
DC2	Mvrcia tomentosa	
	Myrciaria delicatula	
	Myrcian gardnoriang	
DCZ	wyrsine_garanenana	
DC2	Palicourea_tomentosa	unavailable data
DC2	Pouteria_torta	
DC2	Priogymnanthus hasslerianus	
DC2	Randia armata	
DC2	Sanindus sanonaria	unavailable data
DC2	Superior abtuallation	
DCZ	Sideroxyion_oblusijoilum	
DC2	Syagrus_romanzoffiana	unavailable data
DC2	Urera_caracasana	unavailable data
TC1	Aspidosperma australe	
TC1	Aspidosperma_cylindrocarpon	
TC1	Astronium fravinifolium	
	Astronium_jruximjonum	
ICI	Bowaichia_virgiiloides	
TC1	Callisthene_fasciculata	
TC1	Cariniana_estrellensis	
TC1	Combretum leprosum	
TC1	Handroanthus hentanhyllus	
TC1	Handroanthus corratifolius	
	limeteethere shows to set the	
ICI	Himatantnus_obovatus	
TC1	Luehea_divaricata	
TC1	Machaerium_paraguariense	
TC1	Pseudobombax marainatum	
TC1	Qualea narviflora	
	Terminalia alabrascons	
IC1	Triplaris_americana	unavailable data
TC1	Vochysia_cinnamomea	
TC1	Vochysia divergens	
TC1	Vochvsia haenkeana	
TC2	Albizia nionoides	
TC2	Alahaman anatanaifalin	
	Alchornea_castaneljolla	
TC2	Casearía_aculeata	
TC2	Casearia_gossypiosperma	
TC2	Casearia sylvestris	
TC2	Cecronia nachystachya	
TC2	Congifera langsdorffii	
TC2	Copuljeru_luligsuoljjii	
102	cupania_vernalis	
rc2	Curatella_americana	
TC2	Dilodendron_bipinnatum	
TC2	Enterolobium contortisiliquum	
TC2	Guarea auidonia	
TC2	Guazuma ulmifolia	unavailable data
TC2	Humanaga courbaril	unavailable uata
102	nymenueu_courburn	
102	inga_vera	
IC2	Mabea_fistulifera	

## **Cluster Species**

SC3	Inga_laurina	
SC3	Inga_marginata	
SC3	Lachesiodendron_viridiflorum	unavailable data
SC3	Margaritaria_nobilis	
SC3	Matayba_elaeagnoides	
SC3	Matayba_guianensis	
SC3	Pilocarpus_pennatifolius	
SC3	Protium_heptaphyllum	
SC3	Protium_spruceanum	
SC3	Sterculia_striata	
SC3	Swartzia_jorori	
SC3	Tabernaemontana_catharinens	sis
SC3	Trichilia_clausseni	
SC3	Trichilia_hirta	unavailable data
SC3	Zanthoxylum_caribaeum	unavailable data
SC3	Zanthoxylum_fagara	unavailable data
SC3	Zanthoxylum_petiolare	unavailable data
SC3	Zanthoxylum_rhoifolium	unavailable data
SC3	Zanthoxylum_riedelianum	
SC4	Acrocomia aculeata	
SC4	Attalea_speciosa	unavailable data
SC4	Copernicia_alba	
SC4	Euterpe_edulis	
SC4	Syagrus_oleracea	
SC4	Syagrus_romanzoffiana	unavailable data
DC1	Aloysia_virgata	
DC1	Amburana_cearensis	
DC1	Anadenanthera_colubrina	
DC1	Aspidosperma_cuspa	unavailable data
DC1	Aspidosperma_polyneuron	unavailable data
DC1	Aspidosperma_subincanum	
DC1	Aspidosperma_tomentosum	
DC1	Astronium_urundeuva	
DC1	Balfourodendron_riedelianum	
DC1	Bauhinia_cheilantha	
DC1	Bauhinia_longifolia	
DC1	Bauhinia_ungulata	
DC1	Calycophyllum_multiflorum	
DC1	Casearia_gossypiosperma	
DC1	Casearia_rupestris	
DC1	Casearia_sylvestris	
DC1	Ceiba_samauma	
DC1	Combretum_leprosum	
DC1	Commiphora_leptophloeos	unavailable data
DC1	Copaifera_martii	
DC1	Cordia_glabrata	

## **Cluster Species**

TC2	Maprounea_guianensis	
TC2	Ormosia_arborea	
TC2	Protium_heptaphyllum	
TC2	Protium_spruceanum	
TC2	Samanea_tubulosa	
TC2	Siparuna_guianensis	
TC2	Tapirira_guianensis	unavailable data
TC2	Trichilia_elegans	
TC2	Trichilia_pallida	
TC2	Xylopia_aromatica	
TC3	Acrocomia_aculeata	
TC3	Andira_inermis	
TC3	Annona_montana	
TC3	Attalea_speciosa	unavailable data
TC3	Byrsonima_coccolobifolia	
TC3	Byrsonima_verbascifolia	
TC3	Campomanesia_guazumifolia	
TC3	Chomelia_pohliana	
TC3	Chrysophyllum_marginatum	
TC3	Copernicia_alba	
TC3	Cordiera_sessilis	
TC3	Crateva_tapia	unavailable data
TC3	Dendropanax_cuneatus	
TC3	Erythroxylum_cuneifolium	
TC3	Eugenia_florida	
TC3	Eugenia_myrcianthes	
TC3	Eugenia_uniflora	unavailable data
TC3	Genipa_americana	
TC3	Guettarda_viburnoides	
TC3	Hieronyma_alchorneoides	
TC3	Nectandra_cissiflora	
TC3	Nectandra_megapotamica	
TC3	Ouratea_castaneifolia	
TC3	Palicourea_crocea	
TC3	Palicourea_deflexa	unavailable data
TC3	Palicourea_tomentosa	unavailable data
TC3	Pouteria_gardneri	
TC3	Prockia_crucis	
TC3	Psidium_guineense	
TC3	Salacia_elliptica	
TC3	Sapindus_saponaria	unavailable data
TC3	Sideroxylon_obtusifolium	
TC3	Simarouba_amara	
TC3	Vitex_cymosa	
TC3	Ximenia_americana	unavailable data



**Figure S2.** Geomorphology map displaying the geographical distribution of species belonging to each functional cluster across different geomorphological classes in the state of Mato Grosso do Sul.

**Figure S3.** Climate type map showing the geographical distribution of species belonging to each functional cluster across different climate types in the state of Mato Grosso do Sul.





**Figure S4.** Pedology map illustrating the geographical distribution of species belonging to each functional cluster across different soil classes in the state of Mato Grosso do Sul.

**Table S5.** MFA results for the different clusters and environmental variables of pedology, geomorphology, and climate type for the state of Mato Grosso do Sul.

Eigenvalues	Dim.1	Dim.2	Dim.3	Dim.4	Dim.5	Dim.6	Dim.7	Dim.8	
Variance	2.978	0.258	0.211	0.120	0.057	0.029	0.010	0.008	
% of var.	81.126	7.023	5.740	3.258	1.545	0.794	0.285	0.228	
Cumulative % of var.	81.126	88.149	93.889	97.147	98.692	99.486	99.772	100.000	
Groups	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
geomorphology	0.992	33.312	0.977	0.031	11.849	0.001	0.051	24.261	0.003
pedology	0.993	33.345	0.935	0.176	68.108	0.029	0.123	58.343	0.014
climate type	0.993	33.343	0.976	0.052	20.043	0.003	0.037	17.396	0.001
Individuals	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
DC1	3.460	44.657	0.958	-0.255	2.794	0.005	-0.409	8.818	0.013
DC2	0.048	0.009	0.002	0.783	26.421	0.577	0.614	19.905	0.355
SC1	0.726	1.966	0.233	-0.988	42.076	0.432	0.846	37.719	0.316
SC2	1.515	8.562	0.764	0.365	5.746	0.044	-0.439	10.154	0.064
SC3	-1.095	4.477	0.662	0.457	8.988	0.115	0.337	6.001	0.063
SC4	-2.695	27.101	0.957	-0.290	3.624	0.011	-0.407	8.744	0.022
TC1	-1.006	3.773	0.658	-0.276	3.289	0.050	-0.317	5.306	0.065
TC2	-1.496	8.352	0.909	-0.165	1.178	0.011	-0.251	3.320	0.026
TC3	0.544	1.104	0.367	0.369	5.884	0.169	0.026	0.035	0.001

Continuous variables									
(the 10 first)	Dim.1	ctr	cos2	Dim.2	ctr	cos2	Dim.3	ctr	cos2
Dep	0.996	7.379	0.992	-0.032	0.086	0.001	0.000	0.000	0.000
High	0.790	4.648	0.625	0.348	10.378	0.121	0.465	22.771	0.217
Hill	0.968	6.966	0.937	-0.122	1.274	0.015	-0.104	1.130	0.011
Plan	0.989	7.274	0.978	0.023	0.045	0.001	0.036	0.137	0.001
Plateau	0.973	7.045	0.947	0.028	0.065	0.001	-0.046	0.223	0.002
Argi	0.962	3.632	0.925	-0.169	1.303	0.029	0.014	0.011	0.000
Camb	0.935	3.436	0.875	-0.277	3.489	0.077	-0.089	0.444	0.008
Cher	0.954	3.577	0.910	0.033	0.049	0.001	-0.209	2.429	0.044
Gleis	0.787	2.435	0.620	0.509	11.754	0.259	0.021	0.024	0.000
Latos	0.940	3.473	0.884	0.089	0.358	0.008	0.256	3.629	0.065

**SI1.** R code for (I) Performing Clustering analysis and Visualization, (II) Hierarchical Cluster Analysis and Species list by Cluster, (III) Performing Principal Component Analysis (PCA) and Visualization, (IV) Species Occurrence Data Download and Save, (V) Creating Parallel Coordinates Visualisation, and (VI) Multiple Factor Analysis (MFA) and Visualization

#### I. Clustering analysis and Visualisation

```
library(factoextra)
library(ggplot2)
library(dendextend)
library(gridExtra)
library(ggpubr)
load_and_preprocess <- function(file) {</pre>
 data <- read.csv(file)
 clean data <- na.omit(data)
 species_names <- clean_data[, 1]</pre>
 normalized_data <- scale(clean_data[, -1])</pre>
 str(clean data)
 cat(paste("Missing values in", file, ":", any(is.na(normalized_data))), "\n")
 cat(paste("Infinite values in", file, ":", any(is.infinite(normalized_data))), "\n")
 cat(paste("NaN values in", file, ":", any(is.nan(normalized_data))), "\n")
 summary(normalized data)
 head(normalized data)
 return(list(species_names = species_names, normalized_data = normalized_data))
}
decidual_data <- load_and_preprocess("decidual.csv")
semidecidual_data <- load_and_preprocess("semidecidual.csv")
transitional_data <- load_and_preprocess("transição.csv")
titles <- c(expression("A. Deciduous forest"),
      expression("B. Semideciduous forest"),
      expression("C. Transitional forest"))
number_of_clusters <- function(data, title) {</pre>
 plot <- fviz_nbclust(data, kmeans, method = "gap_stat") +</pre>
  labs(title = title)
```

```
set.seed(123)
```

print(plot)

}

```
clusters_decidual <- number_of_clusters(decidual_data$normalized_data, titles[1])
clusters semidecidual <- number of clusters(semidecidual data$normalized data, titles[2])
clusters_transitional <- number_of_clusters(transitional_data$normalized_data, titles[3])
clusters<-grid.arrange(clusters_decidual, clusters_semidecidual, clusters_transitional, ncol = 3)
ggsave("Number of clusters.png", plot = clusters, width = 12, height = 3, units = "in", dpi = 300)
perform kmeans <- function(data, num clusters) {</pre>
 kmeans result <- kmeans(data, num clusters, nstart = 25)
}
results <- mapply(function(data, k) perform kmeans(data, k),
          list(decidual_data$normalized_data, semidecidual_data$normalized_data,
transitional_data$normalized_data),
          c(2, 4, 3), SIMPLIFY = FALSE)
data list <- list(decidual data$normalized data, semidecidual data$normalized data,
transitional data$normalized data)
```

```
clustering_list <- lapply(seq_along(results), function(i) {
fviz_cluster(results[[i]], data = data_list[[i]], repel = TRUE,
        palette = c("#6B7B8E", "#F8b195", "#F67280", "#8FBBAF"),
        ggtheme = theme minimal(), main = titles[i])
```

})

ggsave("Clustering decidual.png", plot = clustering list[[1]], width = 5, height = 4, units = "in", dpi = 300) ggsave("Clustering semidecidual.png", plot = clustering list[[2]], width = 5, height = 4, units = "in", dpi = 300)

ggsave("Clustering transitional.png", plot = clustering\_list[[3]], width = 5, height = 4, units = "in", dpi = 300)

#### II. Hierarchical Cluster Analysis and Species list by Cluster:

res\_decidual <- hcut(decidual\_data\$normalized\_data, k = 2, stand = TRUE) res\_semidecidual <- hcut(semidecidual\_data\$normalized\_data, k = 4, stand = TRUE) res transitional <- hcut(transitional data\$normalized data, k = 3, stand = TRUE)

dend decidual <- as.dendrogram(as.hclust(res decidual)) dend semidecidual <- as.dendrogram(as.hclust(res semidecidual)) dend transitional <- as.dendrogram(as.hclust(res transitional))

```
configure_dendrogram <- function(dend, species_names, colors, k) {</pre>
labels(dend) <- species names
 dend <- color branches(dend, k = k, col = colors)
 dend <- color_labels(dend, k = k, col = colors)
 return(dend)
}
```

```
dend decidual <- configure dendrogram(as.dendrogram(as.hclust(res decidual)),
decidual data$species names, c("#6B7B8E", "#F8b195"), k = 2)
dend semidecidual <- configure dendrogram(as.dendrogram(as.hclust(res semidecidual)),
semidecidual_data$species_names, c("#8FBBAF", "#6B7B8E", "#F8b195", "#F67280"), k = 4)
dend transitional <- configure dendrogram(as.dendrogram(as.hclust(res transitional)),
transitional_data$species_names, c("#8FBBAF", "#6B7B8E", "#F67280"), k = 3)
```

```
visualize_dendrogram <- function(dend, title) {</pre>
 fviz_dend(dend, rect = TRUE, cex = 0.5, k_colors = c("#6B7B8E", "#F8b195", "#F67280", "#8FBBAF"), main =
title, horiz = TRUE)
}
```

```
cluster_dend_decidual <- visualize_dendrogram(dend_decidual, titles[1])
cluster_dend_semidecidual <- visualize_dendrogram(dend_semidecidual, titles[2])
cluster_dend_transitional <- visualize_dendrogram(dend_transitional, titles[3])
cluster_ids_decidual <- cutree(res_decidual, k = 2)</pre>
cluster_ids_semidecidual <- cutree(res_semidecidual, k = 4)
cluster_ids_transitional <- cutree(res_transitional, k = 3)
species_lists <- list(</pre>
lapply(1:2, function(i) decidual_data$species_names[cluster_ids_decidual == i]),
 lapply(1:4, function(i) semidecidual_data$species_names[cluster_ids_semidecidual == i]),
lapply(1:3, function(i) transitional_data$species_names[cluster_ids_transitional == i])
)
save_cluster_to_csv <- function(cluster_list, directory, forest_type) {</pre>
 dir.create(directory, showWarnings = FALSE)
 for (i in seq_along(cluster_list)) {
  cluster_species <- cluster_list[[i]]
  cluster_df <- data.frame(Species = unlist(cluster_species))</pre>
  csv_filename <- file.path(directory, sprintf("%s Cluster %d.csv", forest_type, i))
  write.csv(cluster_df, csv_filename, row.names = FALSE)
}
}
output_dir <- "~/Desktop/Occurrence data/"
save_cluster_to_csv(species_lists[[1]], output_dir, "Decidual")
save_cluster_to_csv(species_lists[[2]], output_dir, "Semidecidual")
save_cluster_to_csv(species_lists[[3]], output_dir, "Transitional")
III. Principal Component Analysis (PCA) and Visualization
calculate_and_visualize_pca <- function(data, title, results) {
 pca_result <- prcomp(data)</pre>
 fviz eig(pca result)
 fviz_pca_biplot(pca_result, col.var = "contrib", select.var = list(contrib = 20), repel = TRUE,
          gradient.cols = c("gray20", "deepskyblue4"),
          geom.ind = "point", pointsize = 1, col.ind = "#758184") +
  labs(title = title) +
  stat_ellipse(aes(fill = as.factor(results[["cluster"]])),
         level = 0.95, geom = "polygon", alpha = 0.25) +
  scale_fill_manual(values = c("#6B7B8E", "#F8b195", "#F67280", "#8FBBAF"), name = "cluster")
}
```

PCA\_decidual<- calculate\_and\_visualize\_pca(decidual\_data\$normalized\_data, titles[1], results[[1]]) PCA\_semidecidual<-calculate\_and\_visualize\_pca(semidecidual\_data\$normalized\_data, titles[2], results[[2]]) PCA\_transitional<-calculate\_and\_visualize\_pca(transitional\_data\$normalized\_data, titles[3], results[[3]])

ggsave("PCA decidual.png", plot = PCA\_decidual, width = 5, height = 4, units = "in", dpi = 300) ggsave("PCA semidecidual.png", plot = PCA\_semidecidual, width = 5, height = 4, units = "in", dpi = 300) ggsave("PCA transitional.png", plot = PCA\_transitional, width = 5, height = 4, units = "in", dpi = 300)

#### IV. Species Occurrence Data Download and Save

install.packages(c("remotes", "rgbif2", "rspecieslink"))

```
remotes::install_github("LimaRAF/plantR")
remotes::install_github("liibre/Rocc")
library(remotes)
library(rgbif2)
library(rspecieslink)
library(plantR)
library(Rocc)
download_and_save_data <- function(csv_path_list, cluster_type) {</pre>
 all_data <- list()
 for (i in seq_along(csv_path_list)) {
  csv_path <- csv_path_list[[i]]
  species_list <- read.csv(csv_path, header = FALSE)[, 1]</pre>
  cat("\nSpecies in Cluster", i, " (", cluster_type, "):\n")
  cat(paste(species_list, collapse = ", "), "\n")
  cluster_data <- lapply(species_list, function(species) {
   occs <- rspeciesLink(species = species)</pre>
   gbif <- rgbif2(species = species)</pre>
   data.frame(
    Species = species,
    Occs = I(list(occs)),
    GBIF = I(list(gbif))
   )
  })
  all_data[[i]] <- do.call(rbind, cluster_data)
  write.csv(all_data[[i]], paste0("cluster_", i, "_", tolower(cluster_type), "_data.csv"), row.names = FALSE)
 }
}
csv_paths <- list(
 "Decidual Cluster 1.csv",
 "Decidual Cluster 2.csv",
 "Semidecidual Cluster 1.csv",
 "Semidecidual Cluster 2.csv",
 "Semidecidual Cluster 3.csv",
 "Semidecidual Cluster 4.csv",
 "Transitional Cluster 1.csv",
 "Transitional Cluster 2.csv",
 "Transitional Cluster 3.csv"
)
download_and_save_data(csv_paths[1:2], "Decidual")
download_and_save_data(csv_paths[3:6], "Semidecidual")
download_and_save_data(csv_paths[7:9], "Transitional")
V. Creating Parallel Coordinates Visualisation
library(ggplot2)
library(GGally)
library(readr)
```

```
my_palette <- c("#abdda4", "#ACDEAA", "#8FBBAF", "#758184", "#6B7B8E",
```

"#F8b195", "#F67280", "#C06c84", "darkred")

```
dados <- read_csv("variaveis.csv")
```

plot\_parallel\_coordinates <- function(data, columns, y\_limits, x\_label, y\_label, title) {</pre>

ggparcoord(data = data,

```
columns = columns,
alphaLines = 0.9,
groupColumn = "Cluster",
showPoints = TRUE,
scale = "globalminmax") +
scale_color_manual(values = my_palette) +
geom_point(size = 3) +
scale_y_continuous(limits = y_limits) +
labs(x = x_label, y = y_label) +
ggtitle(title)
```

}

geomorphology<-plot\_parallel\_coordinates(dados, 2:6, c(-4, 500), "geomorphology", "occurrences", "A. Geomorphology")

pedology<-plot\_parallel\_coordinates(dados, 7:18, c(-4, 350), "pedology", "occurrences", "C. Pedology") climate<-plot\_parallel\_coordinates(dados, 19:23, c(-4, 700), "climate type", "occurrences", "B. Climate type")

ggsave("A. Geomorphology.png", plot = geomorphology, width = 4.5, height = 3, units = "in", dpi = 300) ggsave("C. Pedology.png", plot = pedology, width = 6, height = 3, units = "in", dpi = 300) ggsave("B. Climate type.png", plot = climate, width = 4.5, height = 3, units = "in", dpi = 300)

#### VI. Multiple Factor Analysis (MFA) and Visualisation

```
install.packages(c("FactoMineR", "factoextra", "dplyr", "ggplot2", "rlang"), dependencies = TRUE)
library(FactoMineR)
library(factoextra)
library(dplyr)
library(ggplot2)
library(rlang)
library(readr)
```

dados\_mfa <- na.omit(read.csv("variaveis.csv", row.names = 1))</pre>

```
MFAind <- fviz_mfa_ind(res_mfa, partial = "all", repel = TRUE, palette = c("#8FBBAF",
"#6B7B8E", "#F67280")) + ggtitle("A. Individuals")
MFAvar <- fviz_mfa_var(res_mfa, "quanti.var", col.var = "contrib",
gradient.cols = c("#8FBBAF", "#6B7B8E", "#F67280"),
col.var.sup = "violet", repel = TRUE,
geom = c("point", "text")) + ggtitle("B. Quantitative variables")
```

```
ggsave("A. Individuals.png", plot = MFAind, width = 5, height = 3, units = "in", dpi = 300)
ggsave("B. Quantitative variables.png", plot = MFAvar, width = 5, height = 3, units = "in", dpi = 300)
```

## **APPENDICES**

**Appendix A** - Table 1. Vegetal species evaluated in the study, along with their respective forest of occurrence denoted by the abbreviations DF: Deciduous Forest, SF: Semideciduous Forest, and TF: Transitional Forest, as well as their conservation statuses based on the CNCFlora's red list (Centro Nacional de Conservação da Flora). Where, NE: Not Evaluated, DD: Data Deficient, LC: Least Concern, NT: Near Threatened, VU: Vulnerable, EN: Endangered, CR: Critically Endangered, EW: Extinct In The Wild, EX: Extinct, and NA: (not available) missing data. Extracted from Damasceno-Junior et al. (2018).

Family	id SpeciesName	DF	SF	TF	CNCflora
Acanthaceae	1 Justicia hassleri (Lindau) V.A.W.Graham	x			NE
	2 Ruellia angustiflora (Nees) Lindau ex Rambo	x			NE
	3 Ruellia brevifolia (Pohl) C.Ezcurra	x			NE
Achatocarpaceae	4 Achatocarpus praecox Griseb.	x	х		LC
Anacardiaceae	5 Astronium fraxinifolium Schott		х	х	LC
	6 Astronium graveolens Jacq.		х		LC
	7 Astronium urundeuva (M.Allemão) Engl.	х			LC
	8 Lithraea molleoides (Vell.) Engl.	х			NE
	9 Schinopsis brasiliensis Engl.	х			LC
	10 Schinus terebinthifolia Raddi	x			NE
	11 Spondias mombin L.		х		NE
	12 Tapirira guianensis Aubl.		х	х	NE
Annonaceae	13 Annona coriacea Mart.	х			LC
	14 Annona cornifolia A.StHil.	х			NE
	15 Annona emarginata (Schltdl.) H.Rainer	x			LC
	16 Annona montana Macfad.			х	NE
	17 Annona nutans (R.E.Fr.) R.E.Fr.	х			NE
	18 Annona sylvatica A.St-Hil.		х		NE
	19 Duguetia furfuracea (A.StHil.) Saff.	x		х	NE
	20 Unonopsis guatterioides (A.DC.) R.E.Fr.		х		NE
	21 Xylopia aromatica (Lam) Mart		х	х	LC
Apocynaceae	22 Aspidosperma australe Müll.Arg.			х	LC
	23 Aspidosperma cuspa (Kunth) S.F.Blake ex Pitt	tier x			NE
	24 Aspidosperma cylindrocarpon Müll.Arg.			х	LC
	25 Aspidosperma polyneuron Müll.Arg	х			NT
	26 Aspidosperma pyrifolium Mart.		х		NE
	27 Aspidosperma subincanum Mart.	x			NE
	28 Aspidosperma tomentosum Mart.	х			LC
	29 Hancornia speciosa Gomes.		х		NE
	30 Himatanthus obovatus (Müll.Arg.) Woodson			х	NE
	31 Tabernaemontana catharinensis A.DC.		х		NE
	32 Tabernaemontana siphilitica (L.f.) Leeuwenb		х		NE
Araliaceae	33 Dendropanax cuneatus (DC.) Decne. & Planc	h.	х	х	LC
	34 Didymopanax morototoni (Aubl.) Decne. & F	Planch.	х		NE
Arecaceae	35 Acrocomia aculeata (Jacq.) Lodd		х	х	NE
	36 Allagoptera leucocalyx (Drude) Kuntze			х	NE
	37 Attalea phalerata Mart. ex Spreng.		х	х	LC
	38 Attalea speciosa Mart. ex Spreng.		х	х	NE
	39 Copernicia alba Morong ex Morong & Britto	n	х	х	NE

Family	id SpeciesName	DF	SF	TF	CNCflora
	40 Desmoncus orthacanthos Mart.		х		NE
	41 Euterpe edulis Mart.		х		VU
	42 Syagrus oleracea (Mart.) Becc.		х		NE
	43 Syagrus romanzoffiana (Cham.) Glassman	х	х		LC
Asparagaceae	44 Cordyline spectabilis Kunth & C.D. Bouché		х		NE
Asteraceae	45 Dasyphyllum brasiliense (Spreng.) Cabrera	х	х		NE
	46 Koanophyllon simillimum (B.L.Rob.) R.M.King & H.Rob.	х			NE
	47 Lessingianthus obscurus (Less.) H.Rob.	х			NE
Bignoniaceae	48 Handroanthus heptaphyllus (Vell.) Mattos		х	х	LC
	49 Handroanthus impetiginosus (Mart. ex DC.) Mattos	х			NT
	50 Handroanthus ochraceus (Cham.) Mattos		х		NE
	51 Handroanthus serratifolius (A.H.Gentry) S.Grose	х	х	х	NE
	52 Sparattosperma leucanthum (Vell.) K. Schum.		х		NE
	53 Tabebuia aurea (Silva Manso) Benth. & Hook.f. ex S.Moore		х		NE
	54 Tabebuia nodosa (Griseb.) Griseb.	х			NE
	55 Tabebuia roseoalba (Ridl.) Sandwith	х	х		NE
	56 Zeyheria montana Mart.	х			LC
Burseraceae	57 Commiphora leptophloeos (Mart.) J.B. Gillett	х			NE
	58 Protium heptaphyllum (Aubl.) Marchand		х	х	DD
	59 Protium spruceanum (Benth.) Engl.		х	х	NE
Cactaceae	60 Brasiliopuntia brasiliensis (Willd.) A.Berger	х	х		LC
	61 Cereus bicolor Rizzini & A.Mattos	х	х		NE
	62 Cleistocactus baumannii (Lem.) Lem.	х			NE
	63 Harrisia balansae (K.Schum.) N.P.Taylor & Zappi	х			NE
	64 Pereskia sacharosa Griseb.		х		NE
	65 Praecereus euchlorus (F.A.C.Weber) N.P.Taylor	х			NE
Calophyllaceae	66 Kielmeyera coriacea Mart.		х		NE
Cannabaceae	67 <i>Celtis iguanaea</i> (Jacq.) Sarg.	х			NE
	68 Celtis spinosa Spreng.	х			NE
	69 <i>Trema micrantha</i> (L.) Blume		х		NE
Capparaceae	70 Anisocapparis speciosa (Griseb.) Conejo & Iltis	х			NE
	71 Capparicordis tweediana (Eichler) Conejo & Iltis		х		NE
	72 Capparidastrum coimbranum (Cornejo & Iltis) Cornejo & Iltis.	х	х		NE
	73 Crateva tapia L.			х	NE
	74 Cynophalla mattogrossensis (Pilg.) Cornejo & Iltis	х			NE
	75 Cynophalla retusa (Griseb.) Cornejo & Iltis	х			NE
Caricaceae	76 Jacaratia corumbensis Kuntze.	х			NE
	77 Jacaratia spinosa (Aubl.) A.DC.		x		LC
Celastraceae	78 Monteverdia ilicifolia (Mart. ex Reissek) Biral	х			NE
	79 Salacia elliptica (Mart.) Peyr.			х	NE
Chrysobalanaceae	80 <i>Couepia uiti</i> (Mart. & Zucc.) Benth. ex Hook.f.			х	NE
	81 Hirtella aracilipes (Hook.f.) Prance		х	х	NE
	82 Leptobalanus parvifolius (Huber) Sothers & Prance		х		NE
Cleomaceae	83 <i>Melidiscus giganteus</i> (L.) Raf.		х		NE
Clusiaceae	84 <i>Garcinia brasiliensis</i> Mart.		x		NE
	85 <i>Garcinia aardneriana</i> (Planch, & Triana) Zappi		x		NE
Combretaceae	86 Combretum duarteanum Cambess.	х			NE
	87 Combretum leprosum Mart.	x		x	NF
	88 Terminalia argentea Mart.	~	x		LC

Family	id	SpeciesName	DF	SF	TF	CNCflora
	89	Terminalia corrugata (Ducke) Gere & Boatwr.		х		NE
	90	Terminalia fagifolia Mart.	х			NE
	91	Terminalia glabrescens Mart.		х	х	NE
Cordiaceae	92	Cordia americana (L.) Gottschling & J.S.Mill.	х	х		NE
	93	Cordia brasiliensis (I.M.Johnst.) Gottschling & J.S.Mill.	х			NE
	94	Cordia ecalyculata Vell.		х		NE
	95	Cordia glabrata (Mart.) A.DC.	х			NE
	96	Cordia naidophila I.M. Johnst.	х			NE
	97	Cordia sellowiana Cham		х		NE
	98	Cordia trichotoma (Vell.) Arráb. ex Steud.		х		NE
	99	Varronia grandiflora Desv.		х		NE
Dilleniaceae	100	Curatella americana L.			х	NE
Ebenaceae	101	Diospyros inconstans Jacq.	х			LC
	102	Diospyros tetrasperma Sw.		х		NE
Elaeocarpaceae	103	Sloanea guianensis (Aubl.) Benth.		х		NE
Erythroxylaceae	104	Erythroxylum anguifugum Mart.			х	LC
	105	Erythroxylum cuneifolium (Mart.) O.E. Schulz	х		х	NE
	106	Erythroxylum daphnites Mart.		х		NE
	107	Erythroxylum pelleterianum A.StHil.	х			LC
Euphorbiaceae	108	Acalypha villosa Jacq	х			NE
	109	Actinostemon klotzschii (Didr.) Pax		х		NE
	110	Adelia membranifolia Chod. & Hassl.		х		NE
	111	Alchornea castaneifolia (Willd.) Anderson			х	NE
	112	Alchornea discolor Poepp.		х		NE
	113	Alchornea glandulosa Poepp. & Endl.		х		NE
	114	Alchornea triplinervia (Spreng.) Müll. Arg.		х		NE
	115	Cnidoscolus cervii Fern.Casas	х			NE
	116	Cnidoscolus cnicodendron Griseb.	х			NE
	117	Croton argenteus L.		х		NE
	118	Croton bonplandianus Baill.		х		NE
	119	Croton corumbensis S.Moore		х		NE
	120	Croton floribundus Spreng.		х		NE
	121	Croton gracilipes Baill.	х	х		NE
	122	Croton sellowii Baill.		x		NE
	123	Croton urucurana Baill.		x		NE
	124	Gymnanthes klotzschiana Müll.Arg.		x		NE
	125	Jatropha ellintica (Pohl) Oken		x		NF
	126	Jatropha weddeliana Baill.	x	~		NF
	127	Mahea fistulifera Mart	~		x	NF
	128	Manihot anomala Pohl			x	NF
	120	Manrounea brasiliensis & St -Hil	x		X	NE
	130	Maprounea aujanensis Aubl	x		x	NE
	130	Microstachys danhnoides (Mart ) Müll Ara	X	v	~	NE
	131	Philura hrasiliensis Klatzsch	v	v		NE
	132	Pleradenonhora membranifolia (Müll Ara ) Esser & A. L. Melo	v	~		NE
	124	Sanium alandulosum (1.) Morong	× v			
	125	Sanium haematosnermum Müll Ara	~ ~			
	135	Sanium abayatum Klatzsch ev Müll Ara	~		v	
	127	Sehastiania hrasiliensis Sprena	v		^	
	10/	Sesastania brasilensis spiene.	^			INL

Family	id SpeciesName	DF	SF	TF	CNCflora
	138 Sebastiania ramosissima (A. StHil.) A. L. Melo & M. F. Sales		х		NE
Fabaceae	139 Acosmium cardenasii H.S.Irwin & Arroyo	х			NE
	140 Albizia niopoides (Spruce ex Benth.) Burkart		х	х	LC
	141 Amburana cearensis (Allemão) A.C. Sm.	х			NT
	142 Anadenanthera colubrina (Vell.) Brenan	х			NE
	143 Anadenanthera peregrina (L.) Speg.		х		NE
	144 Andira cujabensis Benth.	х			NE
	145 Andira inermis (W.Wright) Kunth ex DC.			х	NE
	146 Apuleia leiocarpa (Vogel) J.F.Macbr		х		VU
	147 Bauhinia cheilantha (Bong.) Steud.	х			NE
	148 Bauhinia leptantha Malme			х	VU
	149 Bauhinia longifolia (Bong.) Steud.	х			NE
	150 Bauhinia mollis (Bong.) D.Dietr.	х	х		NE
	151 Bauhinia pentandra (Bong.) Vogel ex Steud.	х		х	NE
	152 Bauhinia pulchella Benth.		х		NE
	153 Bauhinia rufa (Bong.) Steud.		х		NE
	154 Bauhinia ungulata L.	х			NE
	155 <i>Bowdichia virgilioides</i> Kunth			х	NT
	156 <i>Calliandra foliolosa</i> Benth.		х		NE
	157 Calliandra parviflora (Hook. & Arn.) Speg.	х			NE
	158 Chloroleucon tortum (Mart.) Pittier		х		NT
	159 Copaifera lanasdorffii Desf.		х	х	NE
	160 <i>Copaifera martii</i> Havne	х			NE
	161 Dalberaia cuiabensis Benth.	х			LC
	162 Dalberaia frutescens (Vell.) Britton	х	х		NE
	163 <i>Dimorphandra mollis</i> Benth.	х			NE
	164 Dintervx alata Vog.		x		LC
	165 <i>Diptychandra aurantiaca</i> (Mart.) Tul.		x		NE
	166 Enterolobium contortisiliquum (Vell.) Morong	х	x	х	NE
	167 Erythrina mulungu Mart.		х		NE
	168 Geoffroea spinosa Jacq.		х		NE
	169 Guibourtia hymenaeifolia (Moric.) J.Léonard	х	х		NE
	170 Holocalyx balansae Micheli		х		NE
	171 Hymenaea courbaril L.			х	LC
	172 Hymenaea martiana Hayne	х			LC
	173 Inga laurina (Sw.) Willd.		х		LC
	174 Inga marginata Willd.		х		NE
	175 Inga vera Willd.			х	NE
	176 Lachesiodendron viridiflorum (Kunth) P.G. Ribeiro, L.P. Queiroz & Luckow	х	х		NE
	177 Leptolobium dasycarpum Vogel		х		NE
	178 Libidibia paraguariensis (D. Parodi) G.P. Lewis	х			NE
	179 Lonchocarpus sericeus (Poir.) Kunth ex DC.	х			NE
	180 Lonchocarpus variabilis R.R.Silva & A.M.G.Azevedo	х			NA
	181 Machaerium acutifolium Vogel	х			NE
	182 Machaerium eriocarpum Benth.	х			NE
	183 <i>Machaerium hirtum</i> (Vell.) Stellfeld	х			NE
	184 Machaerium paraguariense Hassl.			х	LC
	185 Machaerium stipitatum (DC.) Vogel		х		NE
	186 Machaerium villosum Vog.		х		LC

Family	id	SpeciesName	DF	SF	TF	CNCflora
	187	Mimosa adenocarpa Benth.			х	NE
	188	Mimosa bimucronata (DC.) Kuntze		х		NE
	189	Mimosa debilis Humb. & Bonpl. ex Willd.		х		NE
	190	<i>Mimosa glutinosa</i> Malme			х	NE
	191	Mimosa pigra L.		х	х	NE
	192	<i>Mimosa polycarpa</i> Kunth		х		NE
	193	Mimosa weddelliana Benth.			х	NE
	194	<i>Mimosa xavantinae</i> Barneby	х			NE
	195	Muellera nudiflora (Burkart) M.J. Silva & A.M.G. Azevedo		х		NE
	196	Myroxylon balsamum Druce		х		NE
	197	Ormosia arborea (Vell.) Harms	х		х	NE
	198	Parapiptadenia rigida (Benth.) Brenan	х			NE
	199	Parkinsonia praecox (Ruiz & Pav. ex Hook.) J. Hawkins	х	х		NE
	200	Peltophorum dubium (Spreng.) Taub.	х	х		NE
	201	Pityrocarpa moniliformis (Benth.) Luckow & R.W.Jobson			х	NE
	202	Plathymenia reticulata Benth.		х		LC
	203	Platypodium elegans Vogel		х		NE
	204	Prosopis rubriflora Hassl.		х		NE
	205	Prosopis ruscifolia Griseb.	х			NE
	206	Pterogyne nitens Tul.	х			LC
	207	Samanea tubulosa (Benth.) Barneby & J.W. Grimes	х		х	NE
	208	Senegalia polyphylla (DC.) Britton & Rose	х			NE
	209	Senegalia tenuifolia (L.) Britton & Rose	х			NE
	210	Senna pendula (Humb. & Bonpl. ex Willd.) H.S. Irwin & Barneby		х	х	NE
	211	Senna pilifera (Vogel) H.S. Irwin & Barneby	х			NE
	212	Senna silvestris (Vell.) H.S. Irwin & Barneby		х		NE
	213	Senna spectabilis (Vog.) Irw. et Barn.	х			NE
	214	Senna splendida (Vogel) H.S.Irwin & Barneby		х		NE
	215	Sesbania virgata (Cav.) Pers.		х	x	NE
	216	Swartzia jorori Harms.		х		NE
	217	Sweetia fruticosa Spreng.		х		NE
	218	Tachiaali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	х			NT
	219	Vachellia caven (Molina) Seigler & Ebinger	х			NE
	220	Vachellia farnesiana (L.) Wight & Arn.	x		x	NE
	221	Zapoteca formosa (Kunth) H. Hern.	x			NE
	222	Zvaja latifolia (L.) Fawc. & Rendle	x			NE
Heliotropiaceae	223	Myriopus maculatus (Jaca.) Feuillet	x			NE
Lacistemataceae	224	Lacistema hasslerianum Chodat		x	x	NE
Lamiaceae	225	Aegiphilg integrifolig (Jacg.) Moldenke		x		NE
	226	Aeainhila verticillata Vell.	x			NF
	227	Vitex cymosa Bertero ex Spreng	~	x	x	NF
Lauraceae	228	Cinnamomum triplinerve (Ruiz & Pay ) Kosterm		x	~	10
	229	Licaria triandra (Sw.) Kosterm		x		10
	230	Nectandra angustifolia (Schrad ) Nees & Mart		A	x	10
	230	Nectandra cissiflora Nees			x	
	231	Nectandra cusnidata Nees & Mart			x	NF
	232	Nectandra aardneri Meisn.		x	x	NF
	234	Nectandra hihua (R & P.) Rohwer	x	~	~	10
	235	Nectandra meganotamica (Spreng ) Mez	~		x	NF
	-55				~	

Family	id	SpeciesName	DF	SF	TF	CNCflora
	236	Nectandra psammophila Nees			х	LC
	237	Ocotea diospyrifolia (Meisn.) Mez		х	х	NE
	238	Ocotea lancifolia (Schott) Mez	х			LC
	239	Ocotea minarum (Nees & C. Mart.) Mez	х	х		NE
	240	Ocotea velloziana (Meisn.) Mez			х	NE
	241	Persea willdenovii Kosterm.		х		LC
Lecythidaceae	242	Cariniana estrellensis (Raddi) Kuntze		х	х	NE
Loganiaceae	243	Strychnos pseudoquina A.StHil.	х			NE
Lythraceae	244	Adenaria floribunda Kunth		х		NE
	245	Lafoensia pacari A. StHil.		х		LC
Malpighiaceae	246	Bunchosia paraguariensis Nied.	х			NE
	247	Byrsonima clausseniana A. Juss.		х		NE
	248	Byrsonima coccolobifolia Kunth			х	LC
	249	Byrsonima cydoniifolia A. Juss.			х	NE
	250	Byrsonima verbascifolia (L.) Rich.			х	NE
	251	Ptilochaeta nudipes Griseb.	х			NE
Malvaceae	252	Apeiba tibourbou Aubl.		х		NE
	253	, Bastardiopsis densiflora (Hook. & Arn.) Hassl.		х		NE
	254	Byttneria rhamnifolia Benth.		х		NE
	255	Ceiba pubiflora (A. StHil.) K. Schum.	х	х		NE
	256	Ceiba samauma (Mart.) K. Schum.	х			NE
	257	Ceiba speciosa (A. StHil.) Ravenna		х		NE
	258	Guazuma ulmifolia Lam		х	х	NE
	259	Helicteres auazumifolia H.B.K.	x			NE
	260	Helicteres Ihotzkvana (Schott & Endl.) K.Schum.	x	х		NE
	261	Herissantia nemoralis Brizicky		x		IC
	262	Lueheg condicons Mart.		x		10
	263	Luebea divaricata Mart	x	~	x	NF
	264	Luehea arandiflora Mart. & Zuch	~	x	~	NF
	265	Luehea naniculata Mart		x		NF
	266	Pseudabutilan gristulasum (K Schum ) Kranov	x	~		NF
	267	Pseudabutilon benense (Britton) Ervxell	x			NE
	268	Pseudobombax arandiflorum (Cay ) A Robyns	x			
	269	Pseudobombax longiflorum (Martius & Zucc ) A Robyns	x			NF
	200	Pseudobombax marainatum (A St -Hill) A Bobyns	X		x	
	270	Sterculia anetala Karst	×		~	NF
	272	Sterculia striata A St -Hil & Naudin	x	x		NE
	272	Wissadula hernandioides (L. Hér.) Garcke	×	~		NE
Melastomataceae	273	Clidemia hiserrata DC	~	v		NE
	275	Clidemia bullosa DC		~	v	NE
	275	Miconia albicane (Sw.) Stoud		v	^	
	270	Miconia ubicuns (Sw.) steud.	×.	X		
	277	Miconia parvasa (Sm.) Triana	x			
	278	Niconia nervosa (Sill.) Inalia	x			INE
	279		x			INE NE
Meliaceao	280	iococa guianensis Aubi.		X		NE
ואוכוומנשמש	281	Cabralea Canjerana (Vell.) Mart.		х		NE ,
	282			х		VU
	283	Guarea guidonia (L.) Siemer		х	х	NE
	284	Guarea kunthiana A.Juss.		х		NE

Family	id	SpeciesName	DF	SF	TF	CNCflora
	285	Guarea macrophylla Vahl		х		NE
	286	Trichilia catigua A. Juss.	х			NE
	287	Trichilia clausseni C.DC.		х		NE
	288	Trichilia elegans A.Juss.			х	NE
	289	Trichilia hirta L.		х		LC
	290	Trichilia pallida Sw.			х	NE
	291	Trichilia stellato-tomentosa Kuntze	х	х		VU
Menispermaceae	292	Abuta grandifolia (Mart.) Sandwith		х		NE
Moraceae	293	Brosimum gaudichaudii Trec.		х		NE
	294	Ficus adhatodifolia Schott ex Spreng.	х			NE
	295	Ficus broadwayi Urb.		х		LC
	296	Ficus calyptroceras (Miq.) Miq.	х	х		LC
	297	Ficus carautana L.J. Neves & Emygdio			х	EN
	298	Ficus citrifolia Mill.		х		NE
	299	Ficus crocata (Miq.) Miq.			х	NE
	300	Ficus elliotiana S.Moore		х		NE
	301	Ficus eximia Schott	х			LC
	302	Ficus insipida Willd.		x		NE
	303	Ficus Iggoensis C.C. Berg & Carauta	х			NE
	304	Ficus obtusifolia Kunth	x			NE
	305	Ficus pertusa L. f.		x		NE
	306	Maclura tinctoria (L.) D.Don ex Steud.	x	x		NE
	307	Sorocea bonnlandii (Baill.) Burger		x		NF
	308	Sorocea quilleminiana Gaudich.			x	VU
	309	Sorocea sprucei (Baill.) L.F. Macbr.			x	IC
Myrtaceae	310	Blepharocalyx salicifolius (Kunth) O. Berg		x	~	10
	311	Campomanesia augzumifolia (Cambess ) O Berg		~	x	NF
	312	Campomanesia xanthocarna O Berg	x		A	10
	313	Fugenia gurata O Berg	~	x		10
	314	Eugenia bimarainata DC	x	~		NF
	314	Fugenia egensis DC	~	x	x	NE
	315	Eugenia Elorida DC	v	~	v	
	310	Eugenia modesta DC	~		v	NE
	210	Eugenia mucianthes Nield			~	NE
	210	Eugenia nitanga (A. Berg.) Kizersk		v	^	NE
	320	Eugenia prainga (O. Deig.) Maeisk.		~ v		NE
	220	Eugenia pyrjornis Cambess.		~ v		NE
	221	Eugenia reputado. Berg		~		
	322	Eugenia subterninians DC.		^	v	
	323	Eugenia unifiora L.		.,	x	
	324	Eugenia uruguayensis Cambess.		x		INE
	325		X			INE
	320	Myrcia gulanensis (Aubi.) DC.		x		
	327	Wyrcia neolucida A.R.Lourenço & E.Lucas		х		NE
	328	Myrcia selloi (Spreng.) N.Silveira	х			NE
	329	iviyrcia spiendens (SW.) DC.	х			NE
	330	Myrcia tomentosa (Aubi.) DC.	х			NE
	331	Myrcianthes pungens (O.Berg) D. Legrand.		х		LC
	332	Myrciaria delicatula (DC.) O. Berg	х			NE
	333	Myrciaria tenella (DC.) O. Berg		х		DD

Family	id SpeciesName	DF	SF	TF	CNCflora
	334 Plinia peruviana (Poir.) Govaerts			х	NE
	335 Psidium acutangulum DC.	х			NE
	336 Psidium guineense Sw.			х	NE
	337 Psidium hians Mart. ex DC.		х		NE
	338 Psidium kennedyanum Morong.	х		х	NE
	339 Psidium sartorianum (O. Berg) Nied.		х		LC
Nyctaginaceae	340 Bougainvillea glabra Choisy		х		NE
	341 Bougainvillea infesta Griseb.		х		NA
	342 Guapira areolata (Heimerl) Lundell	х			NE
	343 Guapira opposita Vell.		х		NE
	344 Neea hermaphrodita S. Moore	х		х	NE
	345 Pisonia zapallo Griseb.		х		NE
	346 Reichenbachia paraguayensis (D.Parodi) Dugand & Daniel	х			NE
Ochnaceae	347 Ouratea castaneifolia (DC.) Engl.			х	NE
	348 Ouratea purpuripes S. Moore		х		NE
Olacaceae	349 Dulacia papillosa (J.O. Rangel) Sleumer	х			NE
Oleaceae	350 Priogymnanthus hasslerianus (Chodat) P.S. Green	х	х		NE
Opiliaceae	351 Agonandra brasiliensis Miers ex Benth. & Hook. f.	х	х		NE
Phyllanthaceae	352 Hieronyma alchorneoides Allemão	х		х	NE
	353 Margaritaria nobilis L.f.		х		LC
	354 Savia dictyocarpa Müll.Arg.		х		LC
Phytolaccaceae	355 Gallesia integrifolia (Spreng.) Harms		х		NE
	356 Phytolacca dioica L.		х	х	NE
	357 Seguieria aculeata Jacq.		х		NE
	358 Seguieria americana L.	х			LC
Picramniaceae	359 Picramnia latifolia Tul.	х			NE
	360 Picramnia ramiflora Planch.		х		NE
Piperaceae	361 Piper aduncum L.		х	х	NE
	362 Piper amalago L.		х		NE
	363 Piper arboreum Aubl.	х	х	х	NE
	364 Piper cuyabanum C. DC.		х		NE
	365 Piper gaudichaudianum Kunth.		х		NE
	366 Piper glabratum Kunth		х		NE
	367 Piper hispidum Sw.		х		NE
	368 Piper peltatum L.			х	NE
	369 Piper tuberculatum Jacq.			х	NE
Polygonaceae	370 Coccoloba cujabensis Wedd.			х	NE
	371 Coccoloba parimensis Benth.		х		NE
	372 Ruprechtia laxiflora Meisn.		х		NE
	373 Ruprechtia triflora Griseb.		х		NE
	374 Triplaris americana L.	х		х	NE
	375 Triplaris gardneriana Wedd.		х		NE
Primulaceae	376 <i>Clavija nutans</i> (Vell.) B. Ståhl		х	х	NE
	377 Myrsine gardneriana A.DC.	Х			NE
	378 Myrsine guianensis (Aubl.) Kuntze		х		NE
Rhamnaceae	379 Rhamnidium elaeocarpum Reiss.	х	х		NE
	380 Sarcomphalus mistol (Griseb.) Hauenschild		х		NE
Rubiaceae	381 Calycophyllum multiflorum Griseb.	х	х		NE
	382 Calycophyllum spruceanum (Benth.) Hook. f. ex K. Schum.	х			NE

Family	id S	SpeciesName	DF	SF	TF	CNCflora
	383 C	Chomelia pohliana Müll.Arg.			х	NE
	384 C	Cordiera sessilis (Vell.) Kuntze		х	х	NE
	385 C	Coussarea hydrangeifolia (Benth.) Müll.Arg.	х			LC
	386 C	Coutarea hexandra (Jacq.) K. Schum.	х	х		NE
	387 F	Ferdinandusa speciosa (Pohl) Pohl		х	х	NE
	388 6	Genipa americana L.	х		х	LC
	389 6	Guettarda viburnoides Cham. & Schltdl.			х	NE
	390 P	Palicourea crocea (Sw.) Roem. & Schult.			х	NE
	391 P	Palicourea deflexa (DC.) Borhidi			х	NE
	392 P	Palicourea marcgravii A. StHil.	х			NE
	393 P	Palicourea rigida Kunth	х			NE
	394 P	Palicourea tomentosa (Aubl.) Borhidi	х		х	NE
	395 P	Psychotria carthagenensis Jacq.		х		NE
	396 R	Randia armata (Sw.) DC.	х	х		NE
	397 R	Rudaea jasminoides (Cham.) Müll. Arg.		х		VU
	398 F	Rudgeg viburnoides (Cham.) Benth.		x		NE
	399 S	Sabicea aspera Aubl.	x		x	NE
	400.5	Simira hexandra (S.Moore) Steverm.	x	x	~	NF
	401 5	Simira sampajoana (Standl.) Steverm	X	x		NE
	402 7	Tocoveng formosa (Cham & Schltdl) K. Schum		x	x	NE
Rutaceae	402 F	Ralfourodendron riedelianum (Engl.) Engl	×	~	~	NT
	403 E	Senheckia almawillia Kaastra	×	v		NE
	404 L	Schleckia amazonica Kastra	~	v		NE
	405 6			~ v		NE
	400 0	Helietta aniculata Benth	×	^		NE
	407 1		*	v		
	406 6	Pilocarpus poppatifolius Lom	X	x		
	409 P	Anocarpus permatijonus Lem.	X	x		
	410 2	canthoxylum cambdeum Lam.	X	X		INE
	411 2	antnoxylum jagara (L.) Sarg.	X	X		INE LC
	412 2	antnoxylum petiolare A. StHil. & Tul.		х		
	413 2	anthoxylum rholfollum Lam.	Х	х		NE
	414 2	anthoxylum riedellanum Engl.		х		NE
	415 2	<i>Canthoxylum rigidum</i> Humb. & Bonpl. ex Willd.		х		NE
	416 2	anthoxylum sprucei Engl.		х		NE
Salicaceae	417 B	<i>Banara arguta</i> Briq.	х			NE
	418 C	Casearia aculeata Jacq.			х	NE
	419 C	Casearia gossypiosperma Briq.	х		х	LC
	420 C	Casearia obliqua Spreng.		х		NE
	421 C	Casearia rupestris Eichler	х			NE
	422 0	Casearia sylvestris Sw.	х	х	х	NE
	423 P	Prockia crucis P. Browne ex L.		х	х	NE
Continuo	424 X	(ylosma venosa N.E.Br.	х		х	NE
Sapindaceae	425 A	Allophylus edulis (A. StHill.) Radik.		х		NE
	426 A	Allophylus pauciflorus Radkl.	х		х	NE
	427 A	Averrhoidium paraguaiense Radlk.		х		NE
	428 C	Cupania castaneaefolia Mart.			х	NE
	429 C	Cupania vernalis Cambess.			х	NE
	430 <i>L</i>	Diatenopteryx sorbifolia Radlk.	х			NE
	431 <i>L</i>	Dilodendron bipinnatum Radlk.	х		х	LC

Family	id SpeciesName	DF	SF	TF	CNCflora
	432 Diplokeleba floribunda N.E. Br.	х	х		NE
	433 Magonia pubescens A. StHil.	x			LC
	434 Matayba elaeagnoides Radlk.		х		NE
	435 Matayba guianensis Aubl.		х		NE
	436 Melicoccus lepidopetalus Radlk.		х		NE
	437 Sapindus saponaria L.	x		х	NE
	438 Talisia esculenta (A. StHil.) Radlk.		х		NE
Sapotaceae	439 Chrysophyllum gonocarpum (Mart. & Eichler) Engl.	x			NE
	440 Chrysophyllum marginatum (Hook. & Arn.) Radlk.	х	х	х	NE
	441 <i>Pouteria gardneri</i> (Mart. & Miq.) Baehni			х	NE
	442 Pouteria torta (Mart.) Radlk.	х	х		LC
	443 Sideroxylon obtusifolium (Roem. & Schult.) T.D. Penn.	х		х	LC
Simaroubaceae	444 Castela tweedii Planch.	х			EN
	445 Simarouba amara Aubl.		х	х	NE
Siparunaceae	446 Siparuna brasiliensis (Spreng.) A.DC.		х		LC
	447 Siparuna guianensis Aubl.		х	х	NE
Solanaceae	448 Capsicum baccatum L.		х		NE
	449 Cestrum mariquitense Kunth	x			NE
	450 Cestrum obovatum Sendtn.			х	NE
	451 Cestrum schlechtendalii G. Don		х		NE
	452 Cestrum strigilatum Ruiz & Pav.	х		х	NE
	453 Solanum acerifolium Dunal	х			NE
	454 Solanum mauritianum Scop.		х		NE
	455 Solanum riparium Pers.			х	NE
	456 Vassobia breviflora (Sendtn.) Hunz.	х			NE
Styracaceae	457 Styrax camporum Pohl		х		NE
Trigoniaceae	458 <i>Trigonia boliviana</i> Warm.			х	NE
Ulmaceae	459 Phyllostylon rhamnoides (J. Poiss.) Taub.	x			NT
Urticaceae	460 Cecropia pachystachya Trécul		х	х	NE
	461 Urera baccifera (L.) Gaudich.		х		NE
	462 Urera caracasana (Jacq.) Gaudich. ex Griseb.	x			NE
Verbenaceae	463 Aloysia virgata (Ruiz & Pav.) Pers.	x	х		NE
Violaceae	464 Pombalia atropurpurea (A.StHil.) Paula-Souza	х			NE
Vochysiaceae	465 Callisthene fasciculata Mart.			х	NE
	466 <i>Qualea parviflora</i> Mart.			х	NE
	467 Vochysia cinnamomea Pohl			х	NE
	468 Vochysia divergens Pohl			х	NE
	469 Vochysia haenkeana (Spreng.) Mart.			х	NE
Ximeniaceae	470 Ximenia americana L.			х	NE

## Appendix B - Table 2. Consulted databases in TRY database.

Dataset_ID	Dataset	Reference
305	Araucaria Forest Database	Higuchi, P.; Silva, A.C. (2013). Araucaria Forest Database.
89	ArtDeco Database	Cornwell, W. K., Cornelissen, J. H. C., Amatangelo, K., Dorrepaal, E., Eviner, V. T., Godoy, O., Hobbie, S. E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H. M., Santiago, L. S., Wardle, D. A., Wright, I. J., Aerts, R., Allison, S. D., van Bodegom, P., Brovkin, V., Chatain, A., Westoby, M. (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. <i>Ecology Letters</i> , <i>11</i> (10), 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x
431	BAAD: a biomass and allometry database for woody plants	Falster, D. S., Duursma, R. A., Ishihara, M. I., Barneche, D. R., FitzJohn, R. G., Vårhammar, A., Aiba, M., Ando, M., Anten, N., Aspinwall, M. J., Baltzer, J. L., Baraloto, C., Battaglia, M., Battles, J. J., Bond-Lamberty, B., van Breugel, M., Camac, J., Claveau, Y., Coll, L., York, R. A. (2015). BAAD: A Biomass And Allometry Database for woody plants: Ecological Archives E096-128. <i>Ecology</i> , 96(5), 1445–1445. https://doi.org/10.1890/14-1889.1
79	BIOME-BGC Parameterization Database	White, M. A., Thornton, P. E., Running, S. W., & Nemani, R. R. (2000). Parameterization and Sensitivity Analysis of the BIOME–BGC Terrestrial Ecosystem Model: Net Primary Production Controls. <i>Earth Interactions, 4</i> (3), 1–85. https://doi.org/10.1175/1087-3562(2000)004<0003:PASAOT>2.0.CO;2
57	Categorical Plant Traits Database	unpub.
345	CIRAD Selmet Tree LNC Sahel	unpub.
106	Climbing Plants Trait Database	Gallagher, R. V., Leishman, M. R., & Moles, A. T. (2011). Traits and ecological strategies of Australian tropical and temperate climbing plants: Trait comparisons of tropical and temperate climbers. <i>Journal of Biogeography</i> , 38(5), 828–839. https://doi.org/10.1111/j.1365-2699.2010.02455.x
176	Climbing plants trait dataset	Gallagher, R. V., & Leishman, M. R. (2012). A global analysis of trait variation and evolution in climbing plants. <i>Journal of Biogeography, 39</i> (10), 1757–1771. https://doi.org/10.1111/j.1365-2699.2012.02773.x
184	Cold Tolerance, Seed Size and Height of North American Forest Tree Species	unpub.
74	Costa Rica Rainforest Trees Database	Chain-Guadarrama, A., Imbach, P., Vilchez-Mendoza, S., Vierling, L. A., & Finegan, B. (2018). Potential trajectories of old-growth Neotropical forest functional composition under climate change. <i>Ecography</i> , 41(1), 75–89. https://doi.org/10.1111/ecog.02637
74	Costa Rica Rainforest Trees Database	Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., Casanoves, F., Díaz, S., Eguiguren Velepucha, P., Fernandez, F. Licona, J. C., Lorenzo, L., Salgado Negret, B., Vaz, M., & Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropica forests? Testing three alternative hypotheses. Journal of Ecology, 103(1), 191–201. https://doi.org/10.1111/1365-2745.12346
74	Costa Rica Rainforest Trees Database	Finegan, B., Peña-Claros, M., de Oliveira, A., Ascarrunz, N., Bret-Harte, M. S., Carreño-Rocabado, G., Casanoves, F., Díaz, S., Eguiguren Velepucha, P., Fernandez, F. Licona, J. C., Lorenzo, L., Salgado Negret, B., Vaz, M., & Poorter, L. (2015). Does functional trait diversity predict above-ground biomass and productivity of tropica

		forests? Testing three alternative hypotheses. Journal of Ecology, 103(1), 191–201. https://doi.org/10.1111/1365-2745.12347
74	Costa Rica Rainforest Trees Database	unpub.
263	Costa Rican Tropical Dry Forest Trees	Powers, J. S., & Tiffin, P. (2010). Plant functional type classifications in tropical dry forests in Costa Rica: Leaf habit versus taxonomic approaches: Leaf habit and functional traits of dry forest trees. Functional Ecology, 24(4), 927–936. https://doi.org/10.1111/j.1365-2435.2010.01701.x
274	Crown Architecture Database	unpub.
288	CTFS Luquillo Forest Dynamics Plot	Swenson, N. G., Stegen, J. C., Davies, S. J., Erickson, D. L., Forero-Montaña, J., Hurlbert, A. H., Kress, W. J., Thompson, J., Uriarte, M., Wright, S. J., & Zimmerman, J. K. (2012). Temporal turnover in the composition of tropical tree communities: Functional determinism and phylogenetic stochasticity. <i>Ecology</i> , <i>93</i> (3), 490–499. https://doi.org/10.1890/11-1180.1
288	CTFS Luquillo Forest Dynamics Plot	Swenson, N. G., Anglada-Cordero, P., & Barone, J. A. (2011). Deterministic tropical tree community turnover: Evidence from patterns of functional beta diversity along an elevational gradient. <i>Proceedings of the Royal Society B: Biological Sciences, 278</i> (1707), 877–884. https://doi.org/10.1098/rspb.2010.1369
48	Dispersal Traits Database	unpub.
75	ECOQUA South American Plant Traits Database	Blanco, C., Sosinski, E., Santos, B., Silva, M., & Pillar, V. (2007). On the overlap between effect and response plant functional types linked to grazing. <i>Community Ecology</i> , 8(1), 57–65. https://doi.org/10.1556/ComEc.8.2007.1.8
75	ECOQUA South American Plant Traits Database	Duarte, L. da S., Carlucci, M. B., Hartz, S. M., & Pillar, V. D. (2007). Plant dispersal strategies and the colonization of Araucaria forest patches in a grassland-forest mosaic. <i>Journal of Vegetation Science</i> , 18(6), 847–858. https://doi.org/10.1111/j.1654-1103.2007.tb02601.x
75	ECOQUA South American Plant Traits Database	Müller, S. C., Overbeck, G. E., Pfadenhauer, J., & Pillar, V. D. (2007). Plant Functional Types of Woody Species Related to Fire Disturbance in Forest–Grassland Ecotones. <i>Plant Ecology</i> , 189(1), 1–14. https://doi.org/10.1007/s11258-006-9162-z
75	ECOQUA South American Plant Traits Database	Overbeck, G. E. (2005). Effect of fire on vegetation dynamics and plant types in subtropical grassland in southern Brazil. PhD Thesis Technische Universität München.
75	ECOQUA South American Plant Traits Database	Overbeck, G. E., & Pfadenhauer, J. (2007). Adaptive strategies in burned subtropical grassland in southern Brazil. Flora - Morphology, Distribution, Functional Ecology of Plants, 202(1), 27–49. https://doi.org/10.1016/j.flora.2005.11.004
75	ECOQUA South American Plant Traits Database	Pillar, V. D., & Sosinski, E. E. (2003). An improved method for searching plant functional types by numerical analysis. <i>Journal of Vegetation Science</i> , 14(3), 323–332. https://doi.org/10.1111/j.1654-1103.2003.tb02158.x
341	eHALOPH - Halophytes Database (2015)	eHALOPH - Halophytes Database (Version 3.11) Tim Flowers, Joaquim Santos, Moritz Jahns, Brian Warburton and Peter Reed; Available on-line [http://www.sussex.ac.uk/affiliates/halophytes], 2015.
414	eHALOPH - Halophytes Database (2018)	eHALOPH - Halophytes Database (Version 3.11) Tim Flowers, Joaquim Santos, Moritz Jahns, Brian Warburton and Peter Reed; Available on-line [http://www.sussex.ac.uk/affiliates/halophytes], 2017.
77	FAPESP Brazil Rainforest Database	Pillar, V. D., & Sosinski, E. E. (2003). An improved method for searching plant functional types by numerical analysis. <i>Journal of Vegetation Science</i> , 14(3), 323–332. https://doi.org/10.1111/j.1654-1103.2003.tb02158.x
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77	FAPESP Brazil Rainforest Database	unpub.
339	FRED - Fine Root Ecology Database	lversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., Bodegom, P. M., & Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. <i>New Phytologist</i> , 215(1), 15–26. https://doi.org/10.1111/nph.14486
285	Functional traits explaining variation in plant life history strategies	Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C., & Franco, M. (2014). Functional traits explain variation in plant life history strategies. <i>Proceedings of the National Academy of Sciences</i> , 111(2), 740–745. https://doi.org/10.1073/pnas.1315179111
267	Functional Traits for Restoration Ecology in the Colombian Amazon	unpub.
439	Functional Traits of Trees	Paine, C. E. T., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N., Bruelheide, H., Daïnou, K., de Gouvenain, R. C., Doucet, JL., Doust, S., Fine, P. V. A., Fortunel, C., Haase, J., Holl, K. D., Jactel, H., Li, X., Kitajima, K., Koricheva, J., Hector, A. (2015). Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. <i>Journal of Ecology</i> , 103(4), 978–989. https://doi.org/10.1111/1365-2745.12401
377	Functional Traits of Trees in Golfo Dulce, Costa Rica	Chacón-Madrigal, E., Wanek, W., Hietz, P., & Dullinger, S. (2018). Traits indicating a conservative resource strategy are weakly related to narrow range size in a group of neotropical trees. <i>Perspectives in Plant Ecology, Evolution and Systematics, 32</i> , 30–37. https://doi.org/10.1016/j.ppees.2018.01.003
377	Functional Traits of Trees in Golfo Dulce, Costa Rica	Chacón-Madrigal, E., Wolfgang, W., Hietz, P. & Dullinger, S. A stress-tolerance syndrome distinguishes endemic tropical trees from their widespread congeners. Unpublished
357	Functional traits of woody species in the Brazilian semi-arid region	unpub.
130	Global 15N Database	Craine, J. M., Elmore, A. J., Aidar, M. P. M., Bustamante, M., Dawson, T. E., Hobbie, E. A., Kahmen, A., Mack, M. C., McLauchlan, K. K., Michelsen, A., Nardoto, G. B., Pardo, L. H., Peñuelas, J., Reich, P. B., Schuur, E. A. G., Stock, W. D., Templer, P. H., Virginia, R. A., Welker, J. M., & Wright, I. J. (2009). Global patterns of foliar nitrogen isotopes and their relationships with climate, mycorrhizal fungi, foliar nutrient concentrations, and nitrogen availability. <i>New Phytologist</i> , <i>183</i> (4), 980–992. https://doi.org/10.1111/j.1469-8137.2009.02917.x
94	Global A, N, P, SLA Database	Reich, P. B., Oleksyn, J., & Wright, I. J. (2009). Leaf phosphorus influences the photosynthesis–nitrogen relation: A cross-biome analysis of 314 species. <i>Oecologia</i> , 160(2), 207–212. https://doi.org/10.1007/s00442-009-1291-2
436	Global Leaf Gas Exchange Database (I)	Lin, YS., Medlyn, B. E., Duursma, R. A., Prentice, I. C., Wang, H., Baig, S., Eamus, D., de Dios, V. R., Mitchell, P., Ellsworth, D. S., de Beeck, M. O., Wallin, G., Uddling, J., Tarvainen, L., Linderson, ML., Cernusak, L. A., Nippert, J. B., Ocheltree, T. W., Tissue, D. T., Wingate, L. (2015). Optimal stomatal behaviour around the world. <i>Nature Climate Change</i> , <i>5</i> (5), 459–464. https://doi.org/10.1038/nclimate2550

437	Global Leaf Gas Exchange Database (II)	Knauer, J., Zaehle, S., Medlyn, B. E., Reichstein, M., Williams, C. A., Migliavacca, M., De Kauwe, M. G., Werner, C., Keitel, C., Kolari, P., Limousin, J., & Linderson, M. (2018). Towards physiologically meaningful water-use efficiency estimates from eddy covariance data. <i>Global Change Biology</i> , 24(2), 694–710. https://doi.org/10.1111/gcb.13893
87	Global Leaf Robustness and Physiology Database	Niinemets, Ü. (1999). Components of leaf dry mass per area—Thickness and density—Alter leaf photosynthetic capacity in reverse directions in woody plants. New Phytologist, 144(1), 35–47. https://doi.org/10.1046/j.1469-8137.1999.00466.x
87	Global Leaf Robustness and Physiology Database	Niinemets, Ü. (2001). Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. <i>Ecology</i> , 82(2), 453–469. https://doi.org/10.1890/0012-9658(2001)082[0453:GSCCOL]2.0.CO;2
340	Global leaf size dataset	Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, Ü., Reich, P. B., Sack, L., Villar, R., Wang, H., & Wilf, P. (2017). Global climatic drivers of leaf size. <i>Science</i> , <i>357</i> (6354), 917–921. https://doi.org/10.1126/science.aal4760
286	Global Respiration Database	Atkin, O. K., Bloomfield, K. J., Reich, P. B., Tjoelker, M. G., Asner, G. P., Bonal, D., Bönisch, G., Bradford, M. G., Cernusak, L. A., Cosio, E. G., Creek, D., Crous, K. Y., Domingues, T. F., Dukes, J. S., Egerton, J. J. G., Evans, J. R., Farquhar, G. D., Fyllas, N. M., Gauthier, P. P. G., Zaragoza-Castells, J. (2015). Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. <i>New Phytologist</i> , 206(2), 614–636. https://doi.org/10.1111/nph.13253
96	Global Respiration Database	Reich, P. B., Tjoelker, M. G., Pregitzer, K. S., Wright, I. J., Oleksyn, J., & Machado, JL. (2008). Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. <i>Ecology Letters</i> , 11(8), 793–801. https://doi.org/10.1111/j.1461-0248.2008.01185.x
28	Global Seed Mass, Plant Height Database	Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., Pitman, A. J., & Westoby, M. (2005). Factors that shape seed mass evolution. Proceedings of the National Academy of Sciences, 102(30), 10540–10544. https://doi.org/10.1073/pnas.0501473102
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Appendix C - Aims and Scope: Functional Ecology - British Ecological Society

Functional Ecology publishes high-impact papers that enable a mechanistic understanding of ecological pattern and process from the organismic to the ecosystem scale. Because of the multifaceted nature of this challenge, papers can be based on a wide range of approaches. Thus, manuscripts may vary from physiological, genetics, life-history, and behavioural perspectives for organismal studies to community and biogeochemical studies when the goal is to understand ecosystem and larger scale ecological phenomena. We believe that the diverse nature of our journal is a strength, not a weakness, and we are open-minded about the variety of data, research approaches and types of studies that we publish. Certain key areas will continue to be emphasized: studies that integrate genomics with ecology, studies that examine how key aspects of physiology (e.g., stress) impact the ecology of animals and plants, or vice versa, and how evolution shapes interactions among function and ecological traits. Ecology has increasingly moved towards the realization that organismal traits and activities are vital for understanding community dynamics and ecosystem processes, particularly in response to the rapid global changes occurring in earth's environment, and Functional Ecology aims to publish such integrative papers.

## Aims and Scope: Journal of Applied Ecology - British Ecological Society

Journal of Applied Ecology publishes novel, broad-reaching papers on the interface between ecological science and the management of the natural environment. We cover all ecological realms and themes in applied ecology, with a focus on addressing the acute global challenges of mitigating and adapting to climate change, conserving biodiversity, and promoting nature's multifaceted contributions to people. We are particularly interested in articles that use ecological science to inform the policies and practices that (i) mitigate the impact of major anthropogenic stressors, such as habitat loss and ecosystem degradation, invasives, climate change, fire, overexploitation, etc, and (ii) show how nature can be managed to improve well being and sustainability in natural and modified systems.

While we focus primarily on studies involving free-living and non agricultural species, we consider papers involving cultivated species (e.g. crops), domestic species (e.g. livestock), or managed species (e.g. honey bees or farmed fish) as long as they have implications for the management of the natural environment.

We aim to be inclusive of novel approaches and non-standard research, and welcome a range of article types (e.g. reviews, practitioner's perspectives, policy directions, and forum articles challenging existing work); contributions with a methodological focus that have strong potential to change the way applied ecology is conducted; and studies testing ideas outside of field settings, such as laboratory experiments and modeling, as long as they advance the discipline of applied ecology and provide recommendations that inform the management of the natural environment.