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**DIVERSIDADE ESCURA E PERTURBAÇÃO ANTRÓPICA LIGADA A FATORES
ABIÓTICOS E DISTÚRBIOS CRÔNICOS E AGUDOS NAS FLORESTAS SECAS DA
CAATINGA DO CEARÁ**

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CAATINGA DO CEARÁ

Tese submetida à Coordenação do Programa de Pós-graduação em Ecologia e Recursos Naturais, da Universidade Federal do Ceará como requisito para a obtenção de título de Doutor em Ecologia e Recursos Naturais, área de concentração Biogeografia.

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MAGNO DANIEL DE OLIVEIRA GONÇALVES ARAÚJO

DIVERSIDADE ESCURA E PERTURBAÇÃO ANTRÓPICA LIGADA A
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SECAS DA CAATINGA DO CEARÁ

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“Ecologia e espiritualidade são fundamentalmente conectadas, porque a profunda consciência ecológica, em última análise, é a consciência espiritual.”

(Fritjof Capra)

RESUMO

Alcançar as metas de conservação e priorizar os esforços requer métricas apropriadas para quantificar a biodiversidade. A medida mais comumente usada é a riqueza de espécies observada, mas ela não leva em conta a parte ausente do *pool* de espécies, ou seja, a diversidade escura, e nem a completude da comunidade. Por essa razão, avaliar os direcionadores desses índices de diversidade é a base para entender os mecanismos na formação dos padrões de diversidade através das condições abióticas e distúrbios antropogênicos. Também compreender padrões de como as condições abióticas podem estar relacionadas aos distúrbios agudos e crônicos são fundamentais para a Caatinga, já que parte de sua cobertura vegetal está atualmente perdida devido à ocupação humana e o habitat remanescente está sob intensa pressão. Essa tese tem por objetivos (1) mostrar se os diferentes fatores de perda de habitat e distúrbio antropogênico crônico são influenciados por recursos clima e solo e (2) se fatores clima, solo e perturbação influenciam a diversidade observada e escura, completude e “*pool*” de espécies. Utilizamos a base de dados do IFN (“Inventário Florestal Nacional”) que compreende 145 parcelas de 20 km x 20 km da comunidade vegetal da Caatinga do estado do Ceará. Nosso estudo mostra que (i) as atividades humanas tendem a perturbar áreas mais úmidas e desmatar preferencialmente áreas mais úmidas sob solos férteis. Especificamente, áreas com mais recursos para ocupação humana possivelmente levaram a um aumento na densidade de pessoas e animais dentro de locais de vegetação da Caatinga, sustentando uma relação causal entre o assentamento da população humana e a degradação da vegetação da Caatinga. (ii) Em geral, pluviosidade e quantidade de habitat é o que melhor explica a diversidade observada e escura na Caatinga cearense e as formas de vida das plantas tendem a responder de forma diferente às variáveis ambientais. Por exemplo, enquanto a riqueza das árvores tende a ser maior em áreas mais úmidas, as ervas tendem a ser mais ricas em áreas mais secas. Esses resultados destacam a importância de calcular diferentes métricas de riqueza de espécies e considerar diferentes grupos de comunidades vegetais.

Palavras-chave: caatinga; diversidade escura; IFN; recursos; ocupação humana.

ABSTRACT

Achieving conservation goals and prioritizing efforts requires appropriate metrics to quantify biodiversity. The most commonly used measure is the observed species richness, but it does not take into account the missing part of the species pool, i.e., dark diversity, nor the completeness of the community. For this reason, evaluating the drivers of these diversity indices is the basis for understanding the mechanisms in the formation of diversity patterns through abiotic conditions and anthropogenic disturbances. Also understanding patterns of how abiotic conditions may be related to acute and chronic disturbances is critical for the Caatinga, as part of its vegetation cover is currently lost due to human occupation and the remaining habitat is under intense pressure. This thesis aims to (1) show whether the different factors of habitat loss-chronic anthropogenic disturbance are influenced by climate-soil resources and (2) whether climate-soil-disturbance factors influence observed diversity and dark, completeness and the species pool. We used the IFN database (“Inventário Florestal Nacional”), which comprises 145 plots of 20 km x 20 km of the plant community of the Caatinga in the state of Ceará. Our study shows that (i) humans activities tend to disturb wetter areas and preferentially deforest wetter areas under fertile soils. Specifically, areas with more resources for human occupation possibly led to an increase in the density of people and animals within the Caatinga vegetation stands, supporting a causal relationship between the settlement of the human population and the degradation of the Caatinga vegetation. (ii) In general, rainfall and habitat amount best explain the observed and dark diversity in the Caatinga of Ceará, and plant life forms tend to respond differently to environmental variables. For example, while trees tend to be richer in wetter areas, herbs tend to be richer in drier areas. These results highlight the importance of calculating different species richness metrics and considering different groups of plant communities.

Keywords: caatinga; dark diversity; IFN; resources; human occupation.

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LISTA DE ABREVIATURAS E SIGLAS

CAD	Chronic anthropogenic disturbance (Distúrbio Antropogênico Crônico)
DAP	Diâmetro Medido à 1,30 cm em Relação ao Solo
DNIT	Departamento Nacional de Infraestrutura de Transportes
GLM	Generalized linear model (Modelo Linear Generalizado)
IFN	Inventário Florestal Nacional
IBGE	Instituto Brasileiro de Geografia e Estatística
LM	Linear model (Modelo Linear)
MMA	Ministério do Meio Ambiente
OSM	OpenStreetMap
SFB	Serviço Florestal Brasileiro
SDTF	Seasonally dry tropical forest (Floresta Tropical Sazonalmente Seca)
PCA	Principal component analysis (Análise de Componentes Principais)
UFC	Universidade Federal do Ceará

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1 INTRODUÇÃO GERAL

A análise de padrões de riqueza de espécies em grande escala é uma ferramenta importante para ecologia, biogeografia e biologia da conservação (GASTON, 2000). A medida mais comumente usada é, quase sem exceção, quantificar a diversidade local observada de espécies. No entanto, as espécies observadas não refletem o conjunto completo de espécies do habitat de um local, pois algumas espécies permanecerão não detectadas devido aos esforços e recursos limitados de amostragem dos investigadores e ao momento da amostragem (PARTEL, SZAVA-KOVATS & ZOBEL, 2011). Por exemplo, espécies raras e espécies com vida útil muito curta podem ser facilmente ignoradas. Isso é especialmente verdadeiro quando as unidades de amostragem são grandes no espaço e esparsas no tempo. Esse conjunto específico de espécies que pertencem a um conjunto regional (*pool*) de espécies, mas não estão presentes localmente, ou que estão “ausentes” de uma comunidade, mas têm o potencial de se estabelecer são conhecidos como “diversidade escura” (ERIKSSON, 1993; ZOBEL, 1997; ZOBEL *et al.*, 2011; PARTEL, SZAVA-KOVATS & ZOBEL, 2011, 2013; PARTEL, 2014; LEWIS, SZAVA-KOVATS & PARTEL, 2016; PARTEL *et al.*, 2019).

Diversidade escura (PARTEL *et al.*, 1996; PARTEL, SZAVA-KOVATS & ZOBEL, 2011; ZOBEL, 2016) ajuda-nos a entender por que certas espécies estão ausentes e as características de locais que normalmente não possuem muitas espécies que poderiam existir lá (PARTEL *et al.*, 2017). Embora a diversidade observada possa fornecer informações valiosas sobre a riqueza de espécies dentro de um determinado local, identificar esta parte da biodiversidade que supostamente está ausente pode fornecer uma compreensão mais completa dos processos que influenciam a biodiversidade e ajudar a avaliar o potencial de conservação e restauração de habitats locais (LEWIS, SZAVA-KOVATS & PARTEL, 2016; MOESLUND *et al.*, 2016). Nesse sentido, entender e monitorar a diversidade observada e escuras em locais de restauração pode fornecer referências para avaliar e abordar as decisões de manejo (LEWIS, SZAVA-KOVATS & PARTEL, 2016). O objetivo da restauração da comunidade é aumentar a diversidade local às custas da diversidade escura (LANE & TEXLER, 2009.).

Ao comparar as comunidades observadas com as escuras, podemos revelar os processos ecológicos que governam a montagem da comunidade (de BELLO *et al.*, 2012; RIIBAK *et al.*, 2015; LEWIS *et al.*, 2016). Para pertencer à diversidade escura, uma espécie ausente deve ter uma probabilidade razoável de dispersão para o local de estudo, e seus requisitos ecológicos devem corresponder às condições locais (PARTEL, 2014). Assim, uma espécie pode estar

ausente de um local devido a mudanças nas condições abióticas, limitação de dispersão e/ou baixa capacidade competitiva (RIIBAK *et al.*, 2015), apesar de estar presente na região circundante (RONK *et al.*, 2016). As diferenças entre os locais não são evidentes apenas pela diversidade de espécies, pois as comunidades podem hospedar um número igual de espécies, mas diferirem muito em sua diversidade escura (RONK *et al.*, 2016).

Além disso, um índice de completude, ou seja, a proporção de espécies do *pool* regional que se dispersaram e se estabeleceram em um local, pode ser calculado para expressar a diversidade de um local em relação ao seu conjunto de espécies (PARTEL, SZAVA-KOVATS & ZOBEL, 2013). A completude da comunidade é altamente relevante para a conservação, pois é independente do tamanho do *pool* de espécies (PARTEL, 2014). Assim, pode ser importante saber quanto do *pool* de espécies é realizado em um local (ou seja, completude) e se as espécies ausentes são capazes de colonizar os habitats (BELINCHÓN, HEMROVÁ & MUNZBERGOVÁ, 2020). Portanto, um cenário de alta completude (ou seja, alta diversidade observada e baixa diversidade escura) deve ter uma alta prioridade de conservação (LEWIS, SZAVA-KOVATS & PARTEL, 2016).

Além do mais, a maioria dos estudos se concentrou no mapeamento da diversidade escura em macro escala (veja, PARTEL, SZAVA-KOVATS & ZOBEL, 2011; RONK, SZAVA-KOVATS & PARTEL, 2015; LEWIS, SZAVA-KOVATS & PARTEL, 2016; RONK *et al.*, 2016, 2017) e na comparação de métodos para estimar a diversidade escura, por exemplo, os valores dos indicadores de Ellenberg (ELLENBERG *et al.*, 1991; HILL *et al.*, 1999; PARTEL *et al.*, 1996) e o índice de probabilidade de Beals (BEALS, 1984) são os métodos mais comuns. Os valores do indicador Ellenberg estimam diretamente a diversidade escura ou o tamanho do *pool* de espécies, e só pode ser usado quando houver informações suficientes sobre os requisitos de habitat das espécies (de BELLO *et al.*, 2016; LEWIS, SZAVA-KOVATS & PARTEL, 2016; RONK *et al.*, 2016). Em contraste, o índice de probabilidade de Beals usa a distribuição geográfica ou padrões de co-ocorrência de espécies como um *proxy* de seus requisitos ecológicos na formação de padrões de diversidade escura (RONK, SZAVA-KOVATS & PARTEL, 2015; de BELLO *et al.*, 2016; LEWIS, SZAVA-KOVATS & PARTEL, 2016; MOESLUND *et al.*, 2016; RIIBAK *et al.*, 2015; RONK *et al.*, 2016, 2017).

Um dos mecanismos amplamente reconhecidos na formação dos padrões de diversidade escura e observada é através de gradientes ambientais (e.g., clima e solo) devido a mudanças nas condições abióticas (STAN *et al.*, 2019; FLOJGAARD *et al.*, 2020; MAIA *et al.*, 2020). O clima em região semiárida apresenta baixos índices pluviométricos e forte seca sazonal

(definidas como o número de meses de chuva ≤ 100 mm) de seis meses ou mais e, temperatura média anual $>17^{\circ}\text{C}$ (MURPHY & LUGO, 1986; PENNINGTON *et al.*, 2009; ALLEN *et al.*, 2017). As evidências existentes indicam que as variações na biodiversidade são impulsionadas pela precipitação, seca sazonal e temperatura (PORTILLO-QUINTERO *et al.*, 2015; MARKS, MULLER-LANDAU & TILMAN, 2016; ESQUIVEL-MUELBERT *et al.*, 2017; MAIA *et al.*, 2020) e que estão frequentemente associadas a solos férteis, com pH moderado a alto (MURPHY & LUGO, 1986; PENNINGTON *et al.*, 2009).

Características do solo (por exemplo, a fertilidade do solo) pode desempenhar um papel na seleção de espécies do *pool* regional, bem como na estruturação dos padrões de diversidade (LE BAGOUSSE-PINGUET *et al.*, 2017; PINHO *et al.*, 2017). Características edáficas têm sido apontados como relevantes nos padrões das comunidades de plantas devido à sua associação com a disponibilidade hídrica (MARKESTEIJN *et al.*, 2010; PENA-CLAROS *et al.*, 2012; APGAUA *et al.*, 2015; CASTELLANOS-CASTRO & NEWTON, 2015; LE BAGOUSSE-PINGUET *et al.*, 2017). Considerando a importância da disponibilidade de água e o solo para a ocorrência da vegetação, algumas questões emergem sobre como esses mecanismos abióticos produzem os padrões atuais de diversidade observada e escura de espécies (PENNINGTON *et al.*, 2009; PARTEL, SZAVA-KOVATS & ZOBEL, 2011, 2013; SANTOS *et al.*, 2012; SEGOVIA *et al.*, 2020).

A disponibilidade de água (áreas mais úmidas) e solos férteis levaram a maiores densidades populacionais humanas, acelerando o cultivo intensivo de lavouras e a conversão em pastagens para o gado (RITO *et al.*, 2017; SILVA, LEAL & TABARELLI, 2017). Ambientes com mais recursos possivelmente levaram a um aumento na densidade de pessoas e animais dentro dos povoamentos, apoiando uma conexão causal entre as populações humanas rurais e a degradação de ambientes e recursos (LEAL *et al.*, 2005; SANTO *et al.*, 2011). Nesse sentido, a ocupação humana tende a ocorrer primeiro e de forma mais intensa em locais que possuem mais recursos e, assim, distúrbios antrópicos tenderiam a ocorrer nesses locais também. Portanto, outro mecanismo que possivelmente afeta os padrões de diversidade escura e observada são os distúrbios antrópicos que abrangem uma grande variedade de fenômenos, desde a eliminação até a perturbação de habitats locais, como impulsionadores da perda de biodiversidade nos trópicos (MALHI *et al.*, 2014).

Essas descobertas reforçam as noções de que a perturbação aguda (perda do habitat) é a principal causa da perda de biodiversidade e a maior ameaça aos serviços ecossistêmicos em todo o mundo (MELO, 2017; THOMPSON *et al.*, 2017). Embora a densidade humana tenha

sido considerada um importante fator de perda do habitat em países tropicais (AIDE *et al.*, 2013; LAURANCE, SAYER & CASSMAN, 2014; MELO, 2017), ela também deve ser considerada um *proxy* da degradação do habitat (LEAL, ANDERSEN & LEAL, 2014). FAHRIG *et al.* (2003, 2017, 2019, 2021) argumenta que a perda de habitat, é suficiente para explicar os efeitos do desmatamento na perda de biodiversidade e, o efeito da quantidade de habitat na riqueza de espécies será mais forte do que os efeitos combinados do tamanho e isolamento do fragmento. Manchas de vegetação de habitat menores e mais isoladas têm menor riqueza de espécies do que as maiores e menos isoladas (MACARTHUR & WILSON, 1967; HAILA, 2002; LAURANCE, 2008) e a riqueza de espécies em uma parcela de tamanho fixo aumenta com a área total de habitat na "paisagem local" ao redor do fragmento (FAHRIG, 2013; WATLING *et al.*, 2020). Estudos empíricos até o momento sugerem que a perda de habitat tem efeitos grandes e consistentemente negativos sobre a biodiversidade (FAHRIG, 2003, 2013; FLETCHER *et al.*, 2018).

Além do desmatamento, populações rurais de baixa renda vivem amplamente dependentes de recursos florestais para uma subsistência adequada, como a retirada de lenha (SINGH, 1998; DAVIDAR *et al.*, 2010; RIBEIRO *et al.*, 2015). Essa remoção frequente e contínua de pequenas porções de biomassa florestal é conhecida como “distúrbio antropogênico crônico” (*chronic antropogenic disturbance*; CAD) (SINGH, 1998; ARNAN *et al.*, 2018; ANTONGIOVANNI *et al.*, 2020). O CAD é o efeito aditivo de múltiplos estressores antropogênicos que levam a alterações leves, mas contínuas da vegetação e diminui a diversidade de espécies de plantas em florestas tropicais sazonalmente secas (*seasonally dry tropical forest*; SDTFs) (RIBEIRO *et al.*, 2015; ANTONGIOVANNI *et al.*, 2020).

As SDTF já ocuparam grandes quantidades de terras tropicais – até 40% de toda a floresta tropical – antes do desmatamento em grande escala (MURPHY & LUGO, 1986). Em muitos países atualmente possuem menos de 10% de sua extensão original (DRYFLOR, 2016). O interesse ecológico em SDTF aumentou com o reconhecimento de sua ecologia e vegetação distintas entre si (PENNINGTON *et al.*, 2009; DRYFLOR, 2016; ALLEN *et al.*, 2017; STAN *et al.*, 2019;). SDTFs são uma das florestas mais ameaçadas em todo o mundo e são ricas em espécies que lidam com vários distúrbios humanos agudos (por exemplo, perda de floresta) e crônicos (por exemplo, sobrepastoreio e extração de lenha) (RITO *et al.*, 2017). O desmatamento altera e reduz drasticamente a quantidade de habitat, potencialmente causando impactos profundos não somente na diversidade observada (FAHRIG, 2003, 2013, 2017, 2019; FLETCHER *et al.*, 2018; ANTONGIOVANNI, VENTICINQUE, & FONSECA, 2018), mas

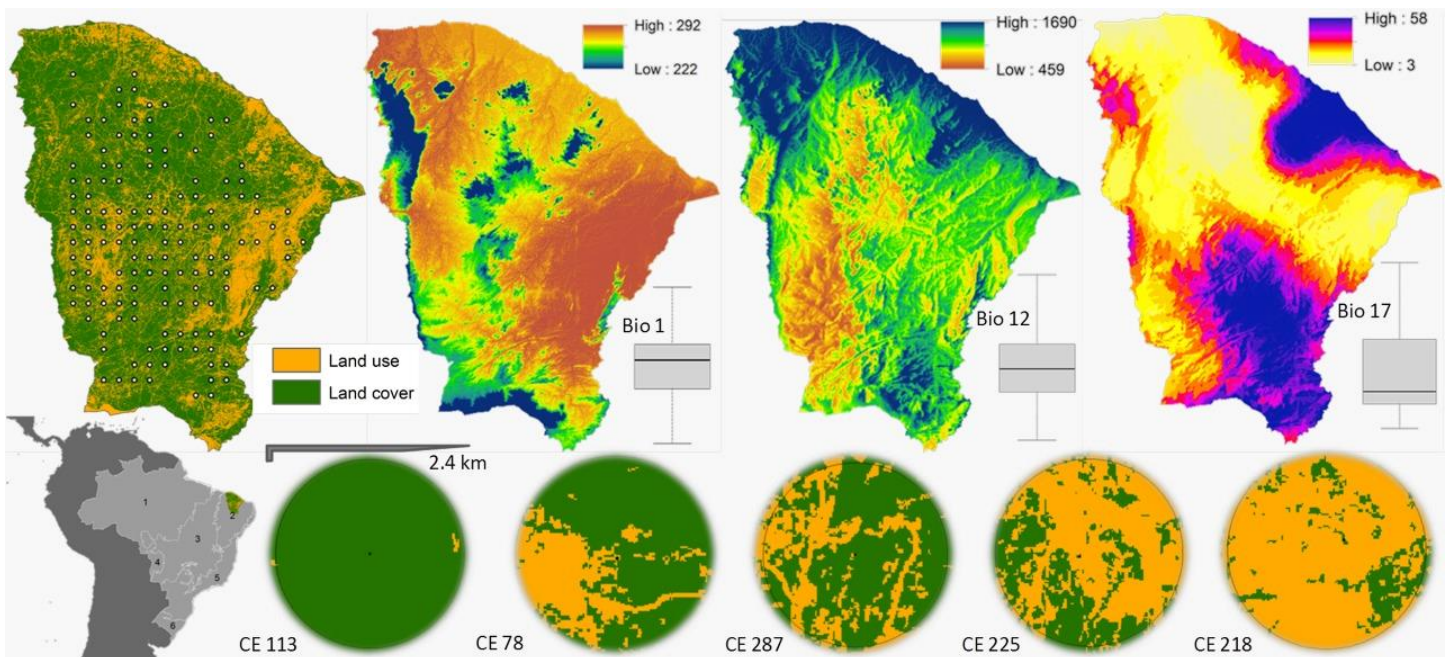
também na diversidade escura, completude e o *pool* de espécies em SDTFs (PARTEL, SZAVAKOVATS & ZOBEL, 2011, 2013; ZOBEL *et al.*, 2011). Portanto, esse é o primeiro estudo em SDTFs na formação dos padrões de diversidade escura.

A maior área contínua de SDTF na América do Sul ocorre no Domínio Fitogeográfico da Caatinga (em aproximadamente 800.000 km²) no nordeste do Brasil (SAMPAIO, 1995; SARKINEN *et al.*, 2011; de ALBUQUERQUE *et al.*, 2012; SILVA *et al.*, 2019). Originalmente ocupando 11% do território brasileiro, a Caatinga localiza-se entre o domínio da Mata Atlântica a leste e com o Cerrado a oeste e sul. Metade de sua cobertura vegetal está atualmente perdida devido à ocupação humana e o habitat remanescente está sob intensa pressão pela extração de lenha, pecuária, produção de carvão, bem como pelo processo de desertificação (MORO *et al.*, 2015; RIBEIRO *et al.*, 2015; MARINHO *et al.*, 2016). Por outro lado, a sazonalidade e distribuição de chuvas, associadas a temperaturas elevadas e condições edáficas altamente variáveis, impulsionam um espectro diversificado de formações fitogeográficas da Caatinga (SAMPAIO, 1995; MORO *et al.*, 2014, 2015). Estas vão desde locais abertos com vegetação arbustiva e herbácea, até áreas onde as espécies arbóreas predominam em riqueza como as Caatingas arbóreas (VELOSO, SAMPAIO & PAREYN, 2002; GRAEFF, 2015; SILVA & SOUZA, 2018). No entanto, os impactos de fatores abióticos regionais-locais e, perturbação aguda e crônica e variações de clima e solo são amplamente desconhecidos na formação dos padrões de diversidade escura, completude e *pool* de espécies para a Caatinga.

Devido às características mencionadas acima, a Caatinga representa um modelo de floresta tropical ideal para estudos para se entender (1) se em áreas com mais distúrbios crônicos e agudos tendem a ocorrer em áreas com mais recursos para populações humanas (maior precipitação e fertilidade do solo), porque existe um grande número de pessoas que vivem na região e suas condições econômicas obrigam muitas comunidades locais a usar recursos naturais para atender às suas necessidades; (2) como os efeitos da perda do habitat, assim como fatores ambientais de clima e solo, na compreensão de padrões não somente na diversidade observada de espécies, mas também para a diversidade escura, completude e *pool* de espécies da comunidade das diferentes formas de vida de plantas (árvores, arbustos, herbáceas e cipós). Estudos recentes indicam que a Caatinga possui 3.347 espécies de plantas das quais 526 (15.72%) são endêmicas (FERNANDES, CARDOSO, & QUEIROZ, 2020) e 350 estão listadas como ameaçadas (MMA, 2016). A vegetação da Caatinga, oferece uma oportunidade interessante para abordar como a floresta tropical sazonalmente seca e biotas semiáridas respondem a alterações humanas do uso da terra como a perda do habitat e distúrbio crônico

antropogênico e também por fatores climáticos e edáficos, a fim de fornecer diretrizes e melhores práticas de conservação da Caatinga em terrenos cristalinos na depressão sertaneja do estado do Ceará.

Essa tese tem por objetivo mostrar variações de perda de habitat, CAD, clima e solo (se áreas com mais perturbação crônica e aguda ocorrem em áreas com mais recurso) e também possíveis influências na diversidade observada e escura, completude e *pool* de espécies da comunidade vegetal da Caatinga do estado do Ceará. A tese está estruturada em dois capítulos. No primeiro capítulo investigamos se, 1. clima e solo influenciam os distúrbios agudos (perda de habitat) e crônicos (CAD) na Caatinga cearense. No segundo capítulo avaliamos se, 1. As variáveis ambientais e de perturbação influenciam a diversidade de plantas e suas diferentes formas de vida na Caatinga cearense? 2. A diversidade escura deve responder de forma diferente em comparação com a diversidade observada? (Fig. 1).



1.1 Figura 1. Localizações de 145 parcelas (pontos brancos) instaladas na Caatinga nas paisagens cristalinas da Depressão Sertaneja do Estado do Ceará. O mapa é derivado de um conjunto de dados raster classificados como habitat (apenas vegetação de Caatinga) e não-habitat (vários usos da terra). A cor verde escura indica vegetação original da Caatinga (land cover) e amarela (land use). Bio1, Bio12 e Bio17 são variáveis climáticas determinantes nos padrões de diversidade de plantas na Caatinga. Os boxplots mostra a variação em média de cada variável climática (ex. Bio1, high: 292 e low: 222). Bio1=temperatura média anual [$^{\circ}\text{C} \cdot 10$], Bio12= precipitação anual [mm/ano] e bio17= precipitação do trimestre mais seco [mm/trimestre]. Os círculos da esquerda para a direita, CE 113, CE 78, CE 287, CE 225 e CE 218, indicam exemplos de paisagens com maior quantidade de habitat (verde) a menor quantidade de habitat (amarelo).

2 CHAPTER 1

2.1 Does anthropogenic disturbance occur in more favorable areas to human occupation?

***Manuscrito a ser submetido na revista “Perspectives in Ecology and Conservation”.**

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ABSTRACT

The interaction of people with the natural environment is ancient. Humans have great power to transform the natural environment and human occupation tends to occur first and most intensively in places that have more resources to agriculture and human settlement, leading chronic disturbance and deforestation. The climate and fertile soils have led to higher human population densities in these places, and with that they increased acute disturbances (habitat loss) caused by the fast conversions of large areas of native vegetation and chronic anthropogenic disturbances (CAD) caused by the slow but continuous overexploitation of the native vegetation. This research aims to highlight if on areas with more resources to human occupation show more disturbance in the Caatinga of the Ceará state. We tested the hypotheses that acute and chronic disturbance would occur in areas with greater rainfall, milder temperatures and greater soil fertility in 143 0.4-ha plots. The results show that humans tend to disturb wetter areas and deforest preferably wetter areas under higher fertile soil, corroborating our hypotheses. Whereas deforestation tend to occur in cooler areas in Caatinga, the chronic anthropogenic disturbance, tend to occur in hotter areas probably because the activities related to chronic disturbance has less income feedback than agriculture and animal husbandry associated to deforestation. Specifically, areas with more resources for human occupation possibly led to an increase in density of people and livestock within the stands of Caatinga vegetation, supporting a causal connection between the human population settlement and the degradation of Caatinga vegetation. Therefore, human disturbance is spatially predictable and cannot be dissociated to environmental variables.

Key words: caatinga; climate; soil; habitat amount; chronic anthropogenic disturbance.

3 INTRODUCTION

Changes in land-use have drastically decreased forest cover worldwide, with research emphasizing perturbation as one of the main threats to tropical biodiversity (LAURANCE, SAYER & CASSMAN, 2014; OSTBERG *et al.*, 2015; SOUZA *et al.*, 2020; BEZERRA *et al.*, 2022) and reduction in species richness (BECKMANN *et al.*, 2019). Tropical forests have been converted into commodity production systems, where logging and other human disturbances as a major threat to biodiversity persistence (CLARK & COVEY, 2012). Particularly the elimination of old-growth forest stands and the expansion of edge-affected habitats in human-modified landscapes, has drastically altered both the availability and quality of tropical forest habitats (FOLEY *et al.*, 2005; HANSEN *et al.*, 2013; LAURANCE, SAYER & CASSMAN, 2014). There is, thus, an urgent need to quantify and predict the ecological effects of anthropogenic disturbance to guide conservation efforts and the management of ecological resources (ARNAN *et al.*, 2018). This is especially true in seasonally dry tropical forests (SDTFs), which are experiencing increased rates of both acute and chronic disturbance (MILES *et al.*, 2006).

Acute disturbance includes habitat loss (MILES *et al.*, 2006) as it usually happens very quickly and transforms the landscape in a manner such that one can easily distinguish the original habitat from the other land uses (FAHRIG, 2003, 2017). Therefore, the acute disturbance represents a major threat to tropical biodiversity caused by the fast conversions of large areas of native vegetation into human-made ecosystems resulting on habitat loss (i.e., remaining habitat amount.) (SINGH, 1998; TSCHARNTKE *et al.*, 2012; SILVA *et al.*, 2017). In contrast to acute human disturbances, chronic anthropogenic disturbance (hereafter referred to as CAD, *sensu* SINGH, 1998; ARNAN *et al.*, 2018; ANTONGIOVANNI *et al.* 2020) include livestock grazing, wood extraction, and the exploitation of miscellaneous forest resources. These activities all result in the removal of biomass through a long time period. CAD is especially prevalent in dry areas of the tropics, where very dense human populations are dependent on forest ecosystems and resources (SINGH, 1998; SPECHT *et al.*, 2015). CAD in fact represent a global pervasive source of disturbance that operates as complementary sources of habitat degradation and species erosion in human-modified landscapes (MAHIRI & HOWORTH, 2001; FAO, 2011).

In addition to deforestation (acute disturbance) and CAD, is well known that environmental variables (e.g., climate and soil) affect plant species diversity (MORO *et al.*,

2015; HILTNER *et al.*, 2016; RITO *et al.*, 2017; De SOUZA *et al.*, 2019; MAIA *et al.*, 2020). Human occupation tends to occur first and most intensively in areas with more resources for agriculture and human settlement (e.g., wetter areas and fertile soils) and therefore deforestation and CAD would occur in this area with possibly greater diversity of species (ALBUQUERQUE *et al.*, 2017; MELO *et al.*, 2017).

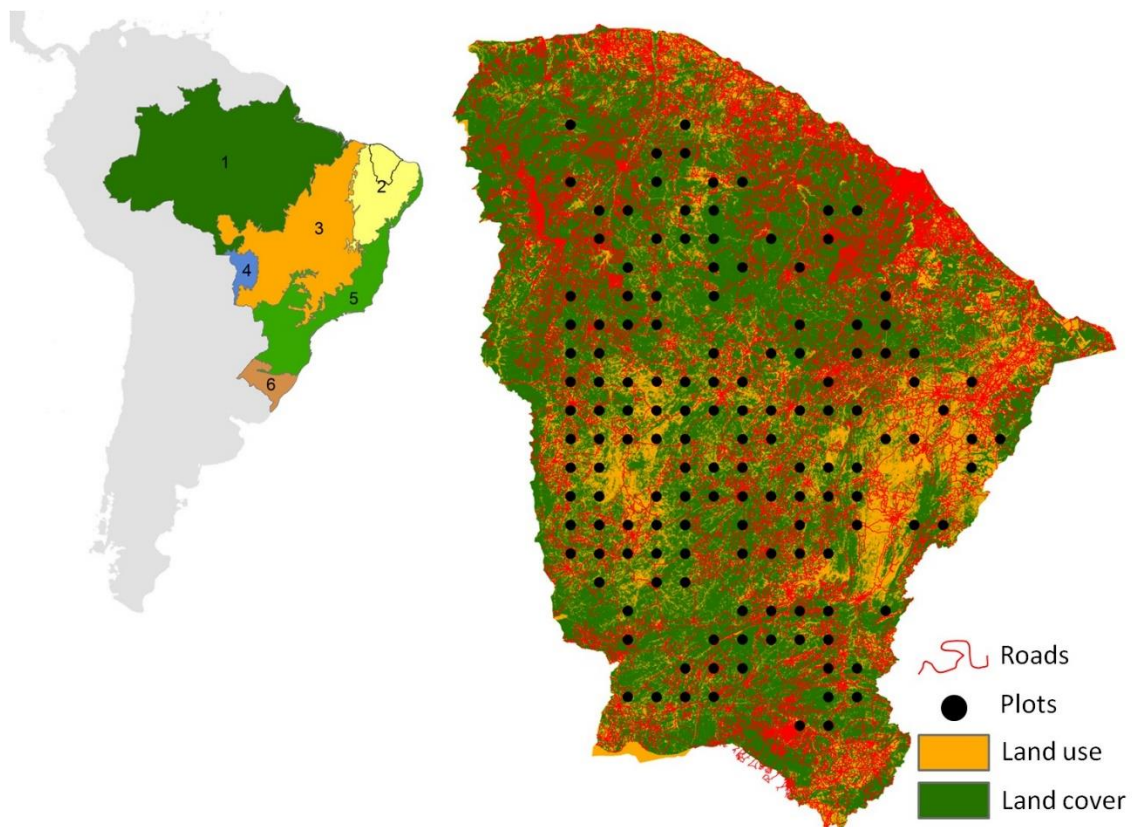
As a SDTF, the Caatinga is under strong anthropogenic pressure (PENNINGTON *et al.*, 2009; RITO *et al.*, 2017). In total, some 22 million people inhabit the Caatinga (BEUCHLE *et al.*, 2015; MARENGO & BERNASCONI, 2015), exerting intensive activities such as subsistence farming, raising domestic livestock, and chronic extraction of timber and non-timber forest products (RIBEIRO *et al.*, 2015, 2016; SOBRINHO *et al.*, 2016; ARNAN *et al.*, 2018). The interactions between populations and nature in the Caatinga have been characterized by an exploration mentality in which natural resources are perceived as infinite and therefore much explored (SILVA, LEAL & TABARELLI, 2017). In the Caatinga, seasonal and inter-annual variations in the rainfall pattern have great influences on the dynamics of human populations (ALBUQUERQUE *et al.*, 2017). The long droughts impose severe conditions on the people, where soil water availability is typically a limiting factor (SANTOS *et al.*, 2014; ALLEN *et al.*, 2017; SILVA, LEAL & TABARELLI, 2017) and the continued land cover transitions in this region, especially related to agriculture, is associated to soil fertility (PEREZ-MARIN *et al.*, 2006).

The relation between human disturbances and natural resources systems are still poorly understood in Caatinga, mainly for studies with soil data. Therefore, we tested the hypothesis that the acute and chronic disturbance tend to occur in areas with greater rainfall, milder temperatures and greater soil fertility. The Caatinga supports dense rural populations, whose livelihoods are heavily dependent on the use of local natural resources; i.e., people living in Caatinga are forest-dependent (SILVA, LEAL & TABARELLI, 2017). Therefore, we ask: 1. do areas with more disturbance (chronic and acute) occur in areas with more resources to human settlement (higher rainfall and more fertile soil)?

4 MATERIAL AND METHODS

4.1 Study area

The caatinga semiarid drylands have rainfall of ca. 300–1000 mm. year⁻¹ (BORGES *et al.*, 2020). It was originally distributed over 826,411 km² of the Brazilian territory according Ministry of the Environment (mapas.mma.gov.br/i3geo/datadownload.htm). The caatinga has high plant diversity, which is partially determined by the aridity gradient (SILVA & SOUZA, 2018). In the state of Ceará, the predominant physiognomy of caatinga is forest (87.7%), covering 7.4 million hectares (SFB, 2019; SOUZA Jr *et al.*, 2020) (Figure 2).



4.1.1 Figure 2. Locations of 143 plots (black circles) installed on the Caatinga sensu stricto in Ceará State by IFN (*Inventário Florestal Nacional*, National Forestry Inventory). The map is a derived from a classified raster dataset. The dark green color indicates original Caatinga vegetation on crystalline formations or habitat (land cover), the orange color indicates non-habitat (agriculture, mines, villages, crops, agriculture and pasture mosaic and other non-vegetated areas) and red indicate roads.

4.2 Sampling design

We used the IFN (“Inventário Florestal Nacional”) database provided by the Brazilian Forest Service (“Serviço Florestal Brasileiro”, SFB, 2019), which comprises 376 grids of 20 km x 20 km (conglomerate) distant at least 20 Km from each other (Fig. 2). Of the 376 points, 233 points were excluded for our analysis, because they were in tropical moist forest, savanna or coast vegetation: we considered only plots installed in the Caatinga vegetation which is a deciduous spiny forest located in crystalline lowlands. Thus, we considered 143 plots located in the Caatinga vegetation in the further analyses.

4.3 Climate data

For each plot we extracted the 19 bioclimatic variables from the CHELSA database. The climate data was used in the station interpolation algorithm of the respective dataset consist of a monthly temperature and precipitation climatology for the years 1979–2013 (KARGER *et al.*, 2017). We considered all climatic variables: bio1= annual mean temperature [$^{\circ}\text{C} \cdot 10$], bio2= mean diurnal range [$^{\circ}\text{C}$], bio3=isothermality, bio4=temperature seasonality [standard deviation], bio5= max temperature of warmest month [$^{\circ}\text{C} \cdot 10$], bio6= min temperature of coldest month [$^{\circ}\text{C} \cdot 10$], bio7=temperature annual range [$^{\circ}\text{C} \cdot 10$], bio8= mean temperature of wettest quarter [$^{\circ}\text{C} \cdot 10$], bio9= mean temperature of driest quarter [$^{\circ}\text{C} \cdot 10$], bio10= mean temperature of warmest quarter [$^{\circ}\text{C} \cdot 10$], bio11= mean temperature of coldest quarter [$^{\circ}\text{C} \cdot 10$], bio12=annual precipitation [mm/year], bio13=precipitation of wettest month [mm/month], bio14=precipitation of driest month [mm/month], bio15=precipitation seasonality [coefficient of variation], bio16=precipitation of wettest quarter [mm/quarter], bio17=precipitation of driest quarter [mm/quarter], bio18=precipitation of warmest quarter [mm/quarter] and bio19=precipitation of coldest quarter [mm/quarter].

4.4 Soil data

Soil data were collected by IFN which comprises 376 grids of 20 km x 20 km (conglomerate) within a radius of up to 2 meters from the central point of each conglomerate,

with samples at a depth of 0-20 cm, using Dutch auger or digger. Soil was collected to verify density, volume and carbon in soil and were stored in resistant plastic bags and sent to a specialized laboratory for analysis. For each site was extracted 16 chemical and physical variables from soil: pH in water, calcium (c. molc.kg⁻¹), magnesium (c. molc.kg⁻¹), aluminum (c. molc.kg⁻¹), potassium (c. molc.kg⁻¹), assimilable phosphorus (mg.kg⁻¹), exchangeable acidity (c. molc.kg⁻¹), potential acidity (c. molc.kg⁻¹), sum of exchangeable bases (c. molc.kg⁻¹), effective cation exchange capacity (c. molc.kg⁻¹), cation exchange capacity at pH 7.0 (c. molc.kg⁻¹), base saturation index (%), aluminum saturation index (%), total carbon by dry combustion (g. kg⁻¹) and clay content (g.kg⁻¹), because they are directly related to soil fertility (LU *et al.*, 2002; SANTOS *et al.*, 2012; SFB, 2019).

For more details, consult the National Forest Inventory Field Manual and forms, available at: <http://www.florestal.gov.br/documentos/informacoes-florestais/inventario-florestal-nacional-ifn/documentos>.

4.5 Remote-sensed habitat classification and pre-processing data

Mapping land use and land cover require regular updates and high spatial resolution data to better understand the historical land use and land cover dynamics, and the subsequent impacts on the country's biomes (PONTIUS & MILLONES, 2011; FONSECA *et al.*, 2017; SOUZA Jr *et al.*, 2020). We considered the limits of the Caatinga under crystalline lowlands from the phytoecological units mapped by MORO, MACEDO & MOURA-FÉ (2015) using the Qgis dissolve tool (QGIS, 2021). The crystalline Caatinga map (MORO, MACEDO & MOURA-FÉ, 2015) was used as a mask layer to cut the Mapbiomas land use and land cover data.

Then, we used georeferenced digital files containing data on vegetation remnants for 2014 according Mapbiomas, with the best updated and accurate image (accuracy = 81.8%) in the last collection published (MAPBIOMAS 5.0, 2019) adjusting the date of the satellite image to the end of 2014, coinciding with the forest inventory in the state of Ceará (SFB, 2019). The Mapbiomas raster and the map of the Caatinga under crystalline using the shapefile by MORO, MACEDO & MOUR-FÉ (2015) were reclassified to create a new raster with habitat (only Caatinga vegetation) and non-habitat using the dissolve layers (union) tool in Qgis (OLSON *et al.*, 2001; MORO, MACEDO & MOURA-FÉ, 2015). The values in the new raster were applied using a defined range of values in pixel classes. The non-habitat category included several land

uses, such as pasture (1,924,517.82 ha, 39.57%), agriculture (497,305.69 ha, 10.22%), agriculture and pasture mosaic (1,642,524.19, 33.77%), temporary crops (217,739.72 ha, 4.48%), urban infrastructure (81,540.90 ha, 1.68%), mining (268.80 ha, 0.005%), perennial crop (279,565.96 ha, 5.75%), soy beans (1.43 ha, 0.00003%), other temporary crops (217,738.30 ha, 4.48%) and other non-vegetated areas (2,853.32 ha, 0.06%) (MAPBIOMAS, 2019; SOUZA Jr *et al.*, 2020).

Additionally, the shapefile composed of a layer paved (provided by DNIT – “*Departamento Nacional de Infraestruturas de Transportes*”; <http://servicos.dnit.gov.br/vgeo>) and unpaved (provided by OSM – *OpenStreetMap*; <http://www.openstreetmap.org/>) roads (IBGE, 2010) were superimposed on the shapefile of the forest remnants to obtain a more accurate scenario of the habitat amount pattern of the Caatinga, since Mapbiomas does not consider roads in their classification. An extension of 110 m for each side of the paved roads and 60 m for each side of the unpaved roads was arbitrarily considered as a deforested area and subtracted from the original forest area (ANTONGIOVANNI *et al.*, 2018).

4.6 Deforestation variables

The cell size of satellite images used to create forest cover maps was 30x30m² (MAPBIOMAS, 2019). A measure of the habitat amount, patch size and isolation effects were estimated for the entire Caatinga landscape in Ceará based on FAHRIG (2013, 2017). We used the “class level metric” in landscape metrics package (HESELBARTH *et al.*, 2019) in R (R CORE TEAM 2019) that returns one value for habitat (Caatinga) and non-habitat (non-Caatinga) in the landscape. The habitat amount is the sum of the area of all patches belonging to Caatinga vegetation (MCGARIGAL, CUSHMAN, & ENE, 2012). The habitat amount was calculated as the percentage of Caatinga vegetation in a predetermined six buffers area around the plot: with 1, 2, 3, 4, 5 and 6 Km of radii.

The patch size data was obtained by measuring the area of patch that contains the plot and isolation was calculated on the basis the nearest-neighbors mean distance of the focal patch to three other patches in the local landscape (FAHRIG, 2013; WATLING *et al.*, 2020). The metrics habitat amount, patch size and isolation effects described were obtained use the landscape metrics package (HESELBARTH *et al.*, 2019) in R (R CORE TEAM 2019).

4.7 Chronic anthropogenic disturbance (CAD)

We used the CAD calculated by ANTONGIOVANNI *et al.* (2020) that was estimated using 14 variables, such as human population, infrastructure, grazing, logging and fire. The variables were carefully selected from a large array of official variables available from Brazilian governmental sources (e.g., IBGE, MMA) to capture relevant, independent dimensions of each vector. A correlation matrix among the 14 variables demonstrated that 96.8% of the 91 estimated correlations were lower than 0.4, supporting their relative independence. All data is available in the Dryad Digital Repository (ANTONGIOVANNI *et al.*, 2020).

The analyzed variables, expressed as distance or density, were used to generate 14 primary surfaces of disturbance along the whole Caatinga territory, each pixel receiving a value corresponding to its disturbance intensity. Therefore, the CAD index data was calculated for each pixel as the weighed sum of the 14 primary variables (d_i , $0 \leq d_i \leq 100$) considering their relative importance (w_i , $0 \leq w_i \leq 1$), standardized by the maximal weighted sum (mws) recorded for a pixel in the whole landscape, including the anthropogenic matrix (ANTONGIOVANNI *et al.*, 2020). Thus, CAD index = $\sum d_i \cdot w_i / mws$ ($1 \geq CDI \geq 0$) where values close to one indicate most disturbed pixel, whereas values close to zero, least disturbed pixel. We used the data published by ANTONGIOVANNI *et al.* (2020) and, for those plots that had no data, we took the closest point to the CAD value index for the Ceará state.

4.8 Data analysis

We used linear models (LMs) with response variables: acute (habitat amount, fragment size, isolation) and chronic (CAD) disturbances and, predictor variables: annual mean temperature, annual mean precipitation, precipitation of driest quarter, base saturation index, assimilable phosphorus and clay content. The response and predictor variables were z-transformed to put the axes on the same scale. To understand how environmental variables are related, we ran principal component analysis (PCA) and analysis of Pearson correlation for climate and soil variables together. We present two PCAs: 1. for climate and soil with all data, 2. for climate and soil for those variables that remained for analysis. Then, we used only the climate + soil variables that are not correlated ($r > -0.7$ and $r < +0.7$) and calculate the loading values for the two main axes and score values in relation to the six axes of the PCA to further analyses. (**Supplementary Material 1**). All analyses were performed in R version 4.4.1 (R

CORE TEAM, 2019), using the package “vegan” (OKSANEN *et al.*, 2016) for construction of PCAs, “corrplot” (WEI & SIMKO, 2021) for the correlation tables, and “visreg” (BREHENY & BURCHETT, 2017) for linear model’s graphs.

5 RESULTS

Our results show that whereas areas under higher mean annual rainfall tend to have higher chronic anthropogenic disturbance, patch isolation, and habitat amount. Those areas under higher mean annual temperature tend to have lower habitat amount, patch isolation and size, but higher chronic anthropogenic disturbance. Soil phosphorous, on the other hand, tend to be negatively related to chronic anthropogenic disturbance and base saturation index, to habitat amount and patch isolation (Table 1; Figure 3). In general, precipitation of driest quarter and clay content variables are poor predictors of acute and chronic perturbation (**Supplementary Material 2**).

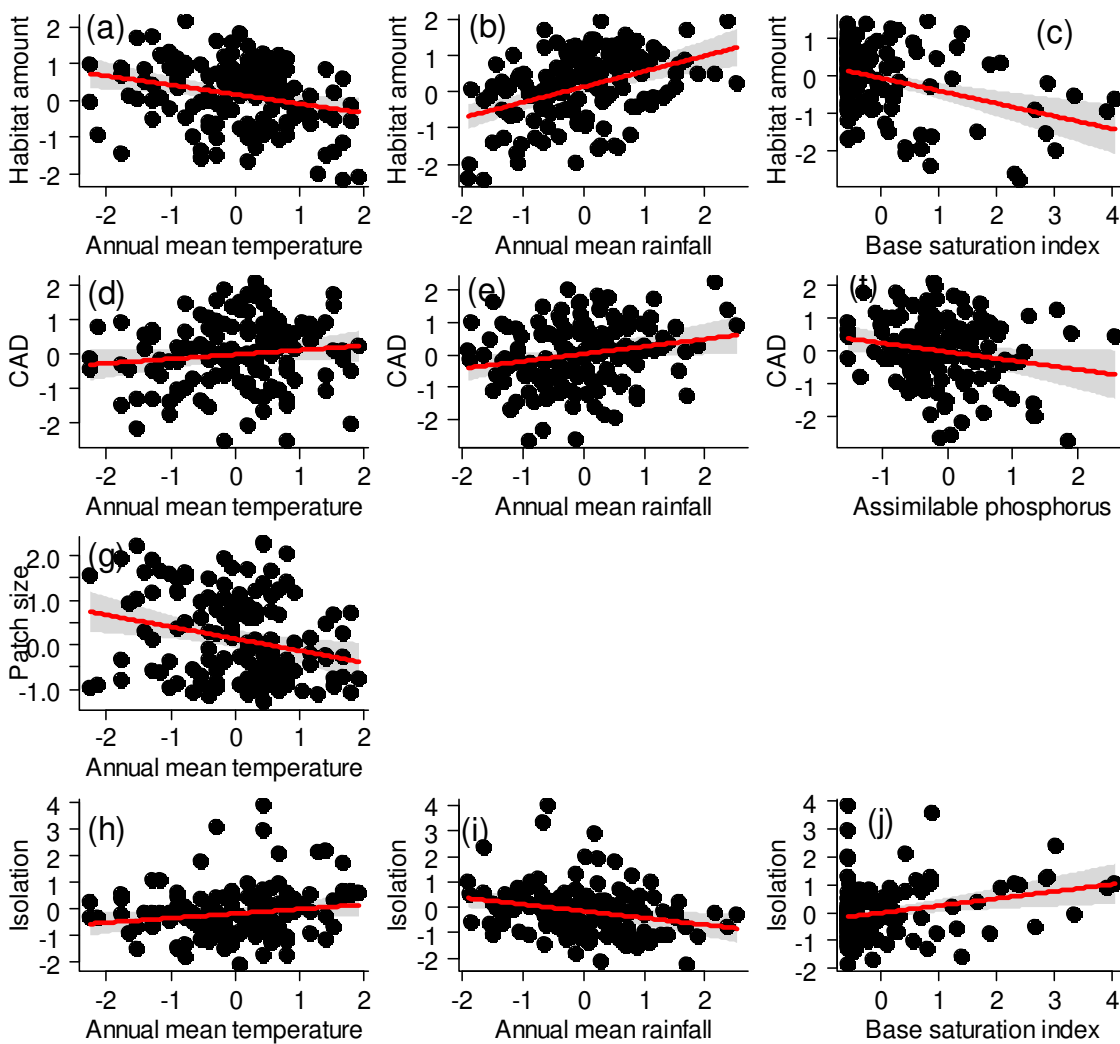
5.1 Table 1. Regression of linear models of habitat amount, chronic anthropogenic disturbance, patch size and isolation using variable of climate and soil as predictor.

Variables	Habitat amount			Chronic anthropogenic disturbance			Df
	Estimate	F value	p	Estimate	F value	p	
Annual mean temperature	-0.25	11.79	0.00 ***	0.12	3.93	0.04 *	141
Annual mean rainfall	0.42	21.75	0.01 ***	0.22	4.60	0.03 *	140
Precipitation of driest quarter	-0.05	0.05	0.82	-0.03	0.11	0.73	139
Clay content	-0.02	0.54	0.46	0.14	0.38	0.53	138
Assimilable phosphorus	0.13	0.34	0.55	-0.26	3.94	0.04 *	137
Base saturation index	-0.33	17.31	0.03 ***	0.05	0.30	0.58	136
Multiple R²	0.28			0.09			

Variables	Patch size			Isolation			Df
	Estimate	F value	p	Estimate	F value	p	
Annual mean temperature	-0.26	12.06	0.00 ***	0.17	5.09	0.02 *	141
Annual mean rainfall	0.09	0.19	0.66	-0.26	4.91	0.02 *	140
Precipitation of driest quarter	-0.14	1.90	0.17	0.11	0.97	0.32	139
Clay content	-0.06	0.01	0.94	0.06	0.05	0.80	138
Assimilable phosphorus	0.14	0.84	0.36	-0.01	0.05	0.81	137

Base saturation index	-0.16	3.50	0.06	0.25	8.29	0.00 **	136
Multiple R²		0.12			0.13		

Note: Explanatory variables are framed according to climate and soil. We use linear model for habitat amount, chronic anthropogenic disturbance, patch size and isolation. R^2 is calculated as $1 - (\text{model deviance}/\text{model null deviance})$ for all response variables. We present the estimate, F value test, the p-value (p) and degrees of freedom (Df).



5.2 Figure 3. Parameter estimates with 95% confidence intervals from the significant environmental variables (climate and soil) predicting habitat amount, chronic anthropogenic disturbance, patch size and isolation. Relationships between the habitat amount and (a) annual mean temperature, (b) annual mean rainfall and (c) base saturation index. Relationships between the chronic anthropogenic disturbance and (d) annual mean temperature, (e) annual mean rainfall and (f) assimilable phosphorus. Relationships between the patch size and (g) annual mean temperature. Relationships between the isolation and (h) annual mean temperature, (i) annual mean rainfall and (j) base saturation index.

6 DISCUSSION

Our study shows that humans tend to disturb wetter areas and deforest preferably wetter areas under higher fertile soil, corroborating our hypotheses. Whereas deforestation tend to occur in cooler areas in Caatinga, the chronic anthropogenic disturbance, tend to occur in hotter areas probably because the activities related to chronic disturbance has less income feedback than agriculture and animal husbandry associated to deforestation. On the other hand, humans disturb areas with less fertile soil because probably because the slash-and-burn agriculture can improve soil fertility. Taken together, our results show that human disturbance is spatially predictable and cannot be dissociated to environmental variables: areas with more resources for human occupation possibly led to an increase in density of people and livestock within the stands of Caatinga vegetation, supporting a causal connection between environmental variables and the degradation of Caatinga vegetation.

There is a preference in deforesting more fertile areas, probably because the soil in the Caatinga regions become appropriate for agriculture and agribusiness when irrigated. Also, because in areas with milder temperatures and more rainfall, there is more vegetation and therefore deforestation would tend to occur preferentially in these places. As a resource becomes scarce, people search for it in other areas, causing increasing habitat loss and converting the few remaining patches of native vegetation into islands within anthropic landscapes. On the other hand, CAD occurs where temperatures are higher, probably because in mild temperatures and wetter areas the financial return activities associated to deforestation is higher, such as agriculture and livestock. In hotter areas, agriculture and livestock on a larger scale do not provide financial returns and only small farms and extraction of non-timber and timber resources are possible.

Habitat loss is the main cause of biodiversity loss and the greatest threat to ecosystem services worldwide (THOMPSON *et al.*, 2017; ANTONGIOVANNI, VENTICINQUE & FONSECA, 2018) because both deforestation and CAD strongly impact the remaining vegetation. Although Caatinga still maintains a reasonable structural integrity, the current remnants are strongly exposed to anthropogenic pressure (RIBEIRO *et al.*, 2015) since human acute disturbance tends to occur in areas with more resources, whereas chronic disturbances in sub-optimal areas for human settlement. Therefore, human component may shape the future of these landscapes in a world where increasingly more tropical forests are embedded into human-dominated landscapes (MELO *et al.*, 2013).

Human population size is a serious threat to the local biodiversity, since Caatinga is one of the most populated drylands of the world (MEDEIROS *et al.*, 2012). Livestock farming is one of the main sources of income and subsistence for the inhabitants and wood extraction for coal, civil construction, and domestic use has been a pervasive threat to the Caatinga (ANTONGIOVANNI, VENTICINQUE & FONSECA, 2018). This is exacerbated by the low mean income of the local population and the high level of inequality, making the natural resources of the Caatinga an essential part of the local population subsistence (GARIGLIO *et al.*, 2010). Understanding natural resource use by human populations is crucial to being able to assess the threats to biodiversity and ecosystem functions properly as well as to design conservation strategies to avoid both ecosystem degradation and depletion of human livelihoods (MELO, 2017).

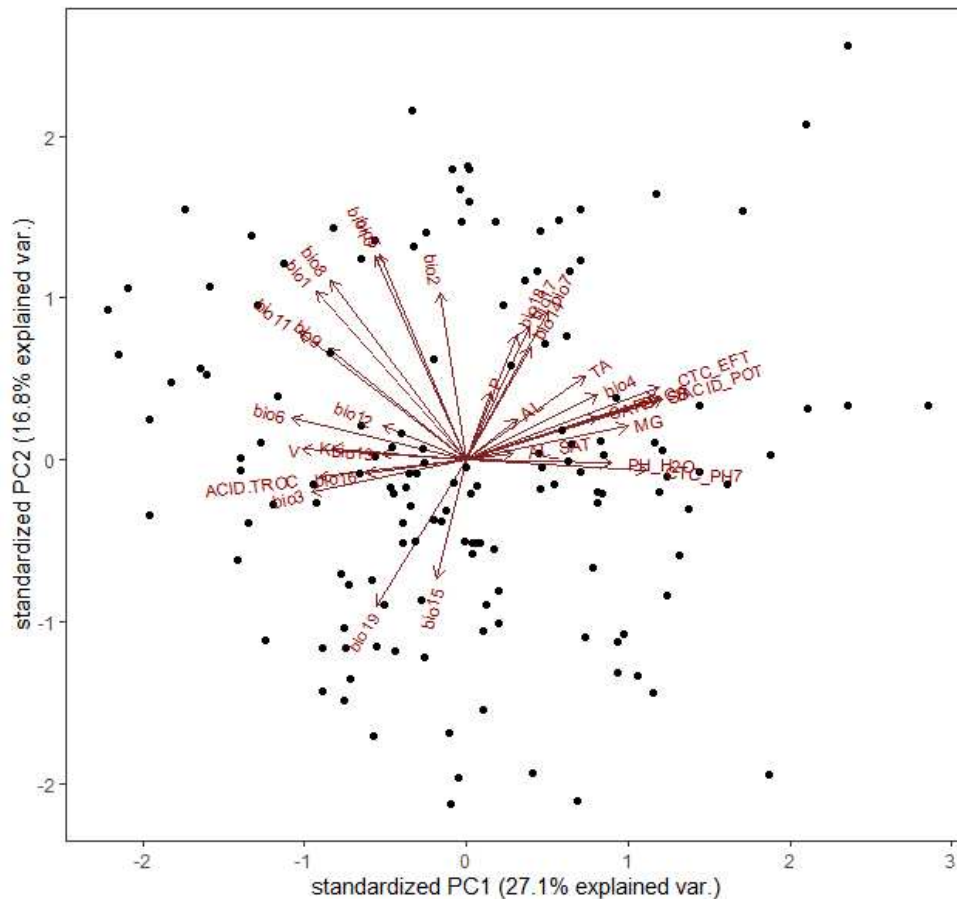
7 CONCLUSION

Given the scenario presented here, we can draw a picture to understand how human disturbance in the Caatinga ecosystem depend on soil fertility and climatic variables (e.g., annual rainfall) that has led to a set of modifications to its original characteristics, with massive deforestation and chronic anthropogenic disturbance. This SDTF is a very resilient ecosystem with centuries of CAD but is currently threatened by large-scale deforestation and expansion of irrigated agriculture (ANTONGIOVANNI, VENTICINQUE & FONSECA, 2018; ANTONGIOVANNI *et al.* 2020). Although acute disturbances are important in understanding the fate of an ecosystem, assessing the role of chronic disturbances is crucial for those biomes

traditionally managed by humans long before the arrival of any agricultural frontiers. These drivers will shape how people use natural resources and therefore the fate of the Caatinga.

SUPPLEMENTARY MATERIAL CHAPTER 1

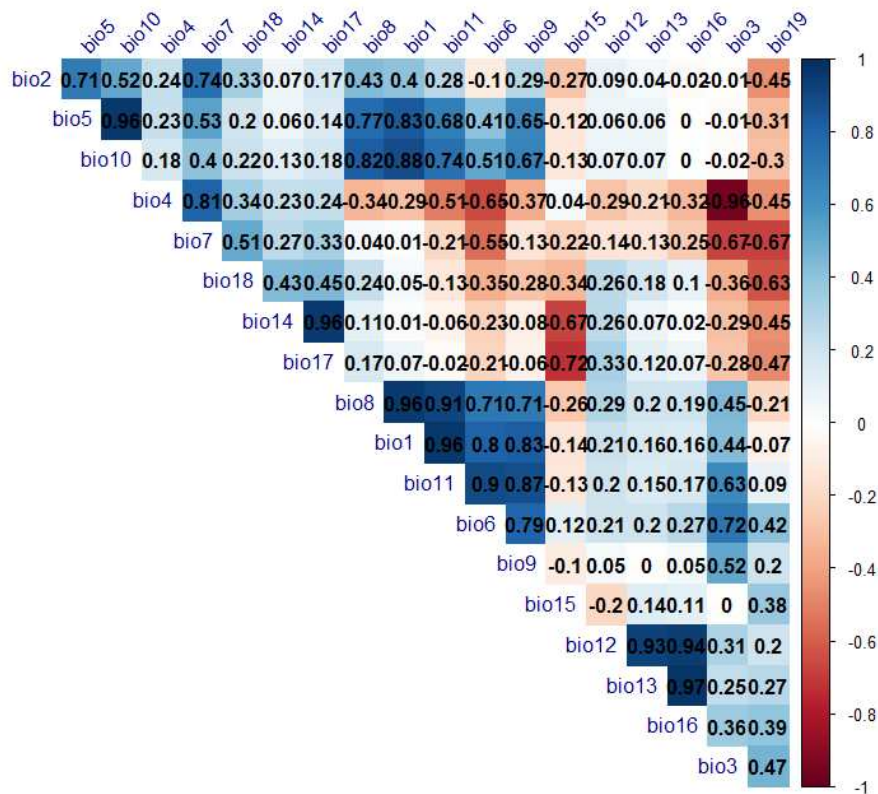
Supplementary Material 1



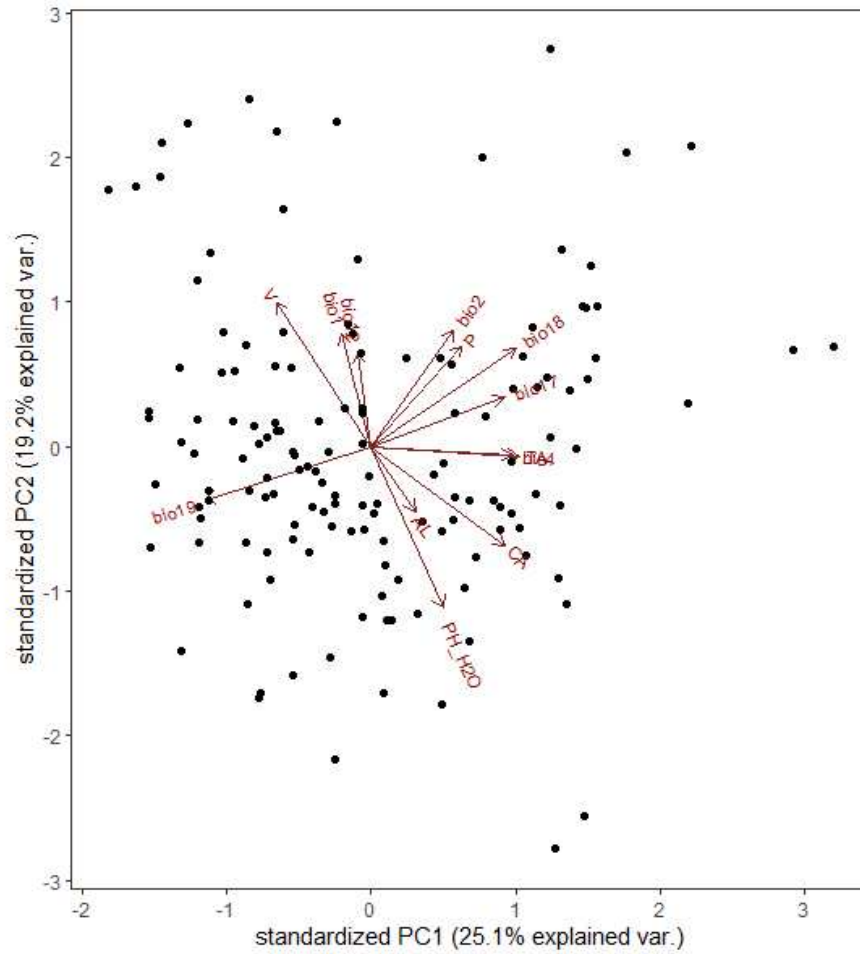
Supplementary Figure 01. PCA with plots for all climate + soil correlated data, bio1= annual mean temperature [$^{\circ}\text{C} \cdot 10$], bio2= mean diurnal range [$^{\circ}\text{C}$], bio3= isothermality, bio4= temperature seasonality [standard deviation], bio5= max temperature of warmest month [$^{\circ}\text{C} \cdot 10$], bio6= min temperature of coldest month [$^{\circ}\text{C} \cdot 10$], bio7= temperature annual range [$^{\circ}\text{C} \cdot 10$], bio8= mean temperature of wettest quarter [$^{\circ}\text{C} \cdot 10$], bio9= mean temperature of driest quarter [$^{\circ}\text{C} \cdot 10$], bio10= mean temperature of warmest quarter [$^{\circ}\text{C} \cdot 10$], bio11= mean temperature of coldest quarter [$^{\circ}\text{C} \cdot 10$], bio12= annual precipitation [mm/year], bio13= precipitation of wettest month [mm/month], bio14= precipitation of driest month [mm/month], bio15= precipitation seasonality [coefficient of variation], bio16= precipitation of

wettest quarter [mm/quarter], bio17=precipitation of driest quarter [mm/quarter], bio18=precipitation of warmest quarter [mm/quarter] and bio19=precipitation of coldest quarter [mm/quarter], pH in water, calcium (CA, c. molc.kg⁻¹), magnesium (MG, c. molc.kg⁻¹), aluminum (AL, c. molc.kg⁻¹), potassium (K, c. molc.kg⁻¹), assimilable phosphorus (P, mg.kg⁻¹), exchangeable acidity (ACID_TROC, c. molc.kg⁻¹), potential acidity (ACID_POT, c. molc.kg⁻¹), sum of exchangeable bases (SB, c. molc.kg⁻¹), effective cation exchange capacity (CTC_EFT, c. molc.kg⁻¹), cation exchange capacity at pH 7.0 (CTC_PH7, c. molc.kg⁻¹), base saturation index (V, %), aluminum saturation index (AL_SAT, %), total carbon by dry combustion (CARB, g. kg⁻¹) and clay content (TA, g.kg⁻¹).

Supplementary Table 01. Correlated and uncorrelated climate variables ($-0.7 < r < + 0.70$): bio1= annual mean temperature [$^{\circ}\text{C} \cdot 10$], bio2= mean diurnal range [$^{\circ}\text{C}$], bio3=isothermality, bio4=temperature seasonality [standard deviation], bio5= max temperature of warmest month [$^{\circ}\text{C} \cdot 10$], bio6= min temperature of coldest month [$^{\circ}\text{C} \cdot 10$], bio7=temperature annual range [$^{\circ}\text{C} \cdot 10$], bio8= mean temperature of wettest quarter [$^{\circ}\text{C} \cdot 10$], bio9= mean temperature of driest quarter [$^{\circ}\text{C} \cdot 10$], bio10= mean temperature of warmest quarter [$^{\circ}\text{C} \cdot 10$], bio11= mean temperature of coldest quarter [$^{\circ}\text{C} \cdot 10$], bio12=annual precipitation [mm/year], bio13=precipitation of wettest month [mm/month], bio14=precipitation of driest month [mm/month], bio15=precipitation seasonality [coefficient of variation], bio16=precipitation of wettest quarter [mm/quarter], bio17=precipitation of driest quarter [mm/quarter], bio18=precipitation of warmest quarter [mm/quarter] and bio19=precipitation of coldest quarter [mm/quarter]. All were $P > 0.05$.

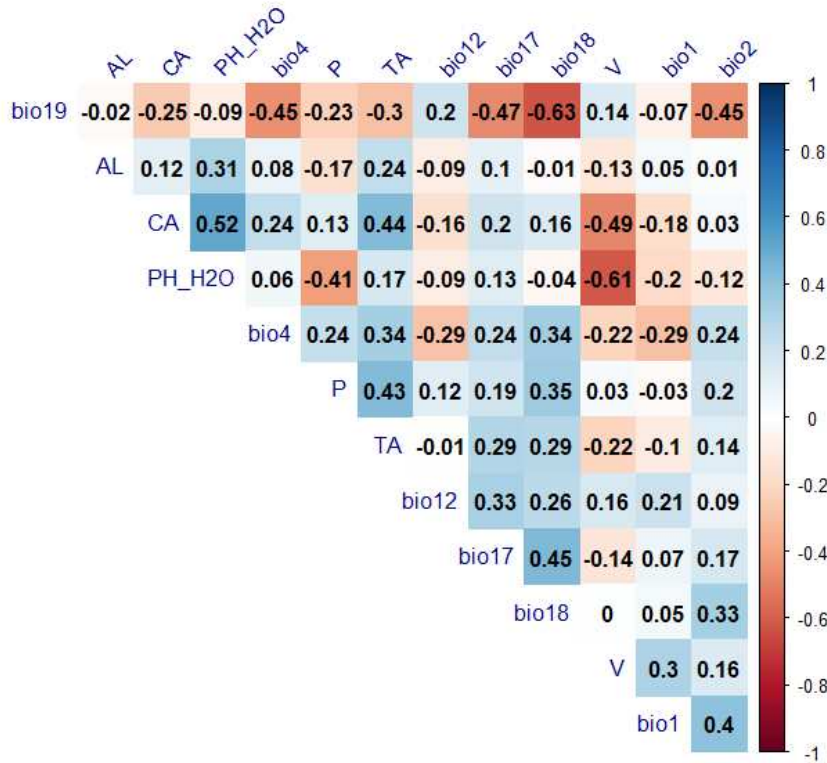


Supplementary Table 02. Correlated and uncorrelated soil variables ($-0.7 < r < + 0.70$): pH in water, calcium (CA, c. molc.kg⁻¹), magnesium (MG, c. molc.kg⁻¹), aluminum (AL, c. molc.kg⁻¹), potassium (K, c. molc.kg⁻¹), assimilable phosphorus (P, mg.kg⁻¹), exchangeable acidity (ACID_TROC, c. molc.kg⁻¹), potential acidity (ACID_POT, c. molc.kg⁻¹), sum of exchangeable bases (SB, c. molc.kg⁻¹), effective cation exchange capacity (CTC_EFT, c. molc.kg⁻¹), cation exchange capacity at pH 7.0 (CTC_PH7, c. molc.kg⁻¹), base saturation index (V, %), aluminum saturation index (AL_SAT, %), total carbon by dry combustion (CARB, g.kg⁻¹) and clay content (TA, g.kg⁻¹).



Supplementary Figure 02. PCA with plots for climate + soil uncorrelated data, bio1= annual mean temperature, bio2= mean diurnal range, bio4=temperature seasonality, bio12=annual precipitation, bio17=precipitation of driest quarter, bio18=precipitation of warmest quarter and bio19=precipitation of coldest quarter, AL= aluminum, P=assimilable phosphorus, TA= clay content, CA= calcium, V= base saturation index and PH_H2O= pH in water.

Supplementary Table 03. Uncorrelated climate + soil variables ($-0.7 < r < +0.70$): bio1= annual mean temperature, bio2= mean diurnal range, bio4=temperature seasonality, bio12=annual precipitation, bio17=precipitation of driest quarter, bio18=precipitation of warmest quarter and bio19=precipitation of coldest quarter, AL= aluminum, P=assimilable phosphorus, TA= clay content, CA= calcium, V= base saturation index and PH_H2O= pH in water. All were $P > 0.05$.



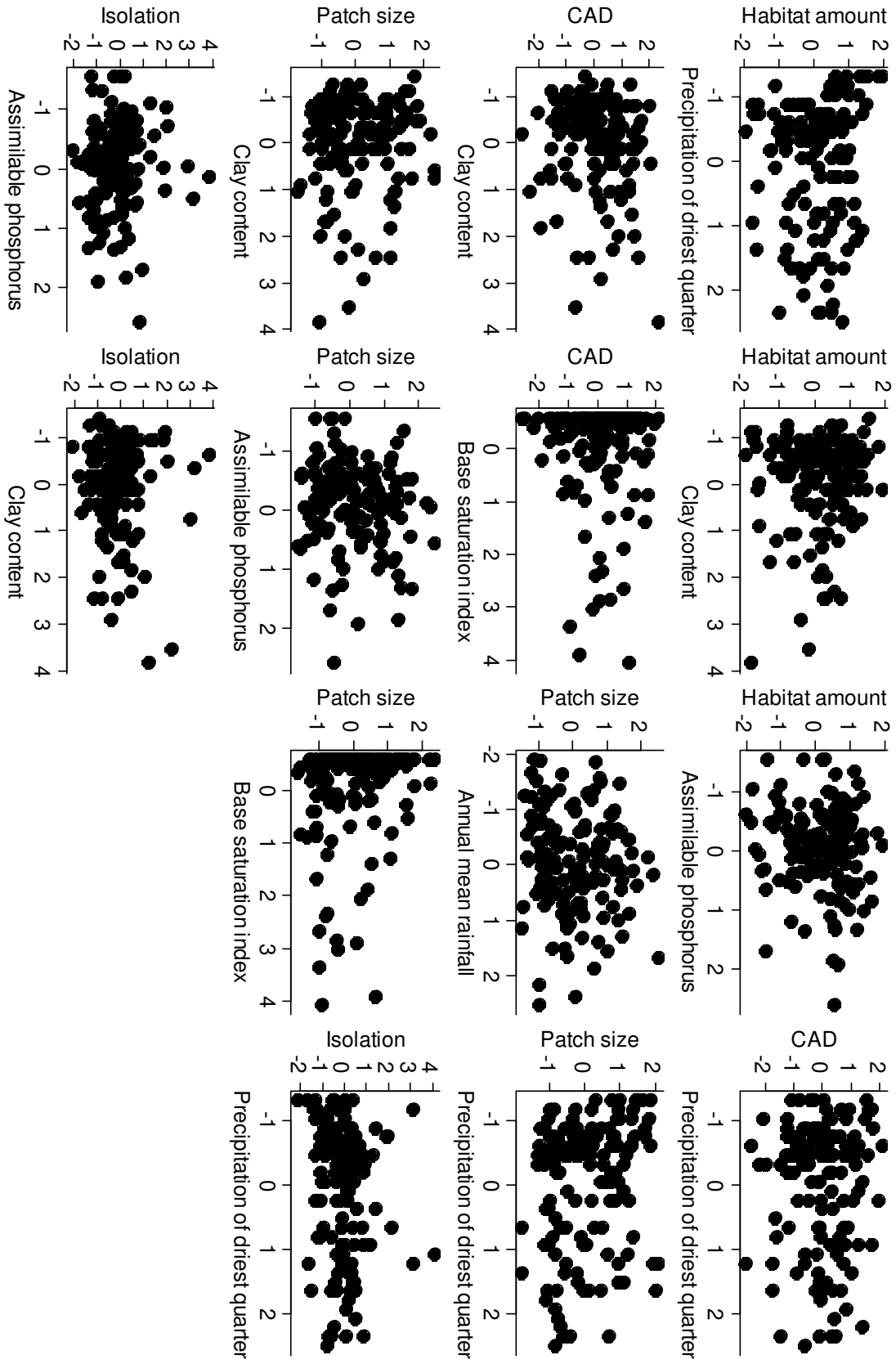
Supplementary Table 04. Loading values for climate + soil for the two main axes of the PCA.

	PC1	PC2
bio1	-0.07	0.32
bio2	0.20	0.33
bio4	0.35	-0.02
bio12	-0.03	0.26
bio17	0.33	0.14
bio18	0.36	0.28
bio19	-0.41	-0.15
AL	0.11	-0.18
P	0.22	0.28
TA	0.37	-0.02
CA	0.33	-0.28
V	-0.23	0.41
PH_H2O	0.18	-0.46

Supplementary Table 05. Score values for each climate + soil variables in relation to the six axes.

Scores	PC1	PC2	PC3	PC4	PC5	PC6
bio1	-0.24	0.93	-0.96	0.60	-0.34	0.60
bio2	0.67	0.96	-0.31	0.85	-0.08	0.48
bio4	1.17	-0.06	0.78	0.42	0.14	-0.50
bio12	-0.11	0.77	-0.94	-1.14	0.10	-0.10
bio17	1.09	0.41	-0.66	-0.47	0.38	-0.46
bio18	1.19	0.80	-0.13	-0.18	0.45	-0.28
bio19	-1.37	-0.44	-0.04	-0.63	-0.51	0.01
AL	0.36	-0.53	-0.73	0.48	-1.00	-0.90
P	0.74	0.83	0.78	-0.68	-0.61	0.34
TA	1.22	-0.07	0.11	-0.38	-0.99	0.06
CA	1.10	-0.81	-0.10	-0.19	-0.18	0.77
V	-0.78	1.19	0.12	0.25	-0.28	-0.39
PH_H2O	0.59	-1.33	-0.80	0.05	0.26	0.16

Supplementary Material 2



Supplementary Figure 03. Non-significant models for deforestation and chronic anthropogenic disturbance (CAD) and, climate and soil variables.

8 CHAPTER 2

8.1 Dark diversity reveals the importance of climate, soil and disturbance for Caatinga plant diversity.

***Manuscrito a ser submetido na revista “Biodiversity and Conservation”.**

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ABSTRACT

Species richness is the most commonly used metric to quantify biodiversity. However, examining dark diversity, the group of missing species which can potentially inhabit a site, can provide a more thorough understanding of the factors influencing biodiversity species assembly. In this study we aim to understand how climate, soil, acute, and -chronic-disturbance factors affect not only species richness but also dark diversity, completeness and species pool patterns of Caatinga on the crystalline landscapes to the Ceará state. We tested the hypothesis that plant diversity, completeness and species pool increase and dark diversity decrease with larger patches, less isolated patches landscapes surrounded by more habitat, with lower chronic anthropogenic disturbance, wetter and hotter climate, and higher soil fertility across 144 0.4-ha plots for trees and 0.04-ha plots for shrubs, herbs and vines provided by the Brazilian Forest Service. We recorded 2148 stems from 317 species. In general, rainfall and habitat amount had positive effects on observed and dark diversity, completeness and species pool for trees, shrubs and vines, excepted for herbs probably due to higher water resource and higher species dispersal in areas with more habitat. Habitat amount is important for observed plant richness, indicating that large patches probably promote the coexistence of plant species and decrease dark diversity. The different metrics of species diversity and the life-forms also tend to respond differently to environmental variables. For instance, whereas the richness of trees tends to be higher in wetter, herbs tend to richer in drier areas. These results highlight the importance to calculate different metrics of species richness and consider different groups of plant communities.

Key words: caatinga; climate; completeness; dark diversity; Seasonally Dry Tropical Forests.

9 INTRODUCTION

In general, studies have been based on observed species records from field sites to predict the response of species to abiotic factors and anthropogenic disturbance (ALLEN *et al.*, 2017; SFAIR *et al.*, 2018; STAN *et al.*, 2019; SOUZA *et al.*, 2019; MAIA *et al.*, 2020). However, the observed species do not reflect the complete “habitat-specific species pool”, as some species will remain undetected due to investigators' limited sampling efforts and resources and the timing of sampling (PARTEL, SZAVA-KOVATS & ZOBEL, 2011; TANG *et al.*, 2019). Here we refer to the “habitat-specific species pool” (hereafter called “species pool” for simplicity), which includes all the species in a region that can inhabit the ecological conditions at a target site and defines species pools in terms of species habitat preferences. The species that are not recorded at a target site, but belong to its species pool, constitute the “dark diversity” of that site (PARTEL, SZAVA-KOVATS & ZOBEL, 2011), which like the dark matter in the universe is known to exist but is not visually observable (de BELLO *et al.*, 2016). While observed diversity can provide valuable information about species richness within a given location, it doesn't account for the absent part of species pool (PARTEL, SZAVA-KOVATS & ZOBEL, 2011). This particular set of species that belong to a species pool but are not locally present are known as “dark diversity”. Therefore, dark diversity focuses on the portion of diversity potentially able to occur in a particular habitat type, but which is currently missing. Dark diversity is calculated by subtracting local diversity from the species pool size (PARTEL, SZAVA-KOVATS & ZOBEL, 2011, 2013; RONK *et al.*, 2015, 2016; LEWIS, SZAVA-KOVATS & PARTEL, 2016).

Dark diversity can also be used to derive community completeness, defined as the proportion of local diversity in relation to its species pool size are affiliated with specific habitat condition (ZOBEL, 1997; ERIKSSO, 1993; ZOBEL *et al.*, 2011; PARTEL, SZAVA-KOVATS & ZOBEL, 2013; BENNETT *et al.*, 2016; ZOBEL, 2016; ANING, 2017) and calculated as a natural logarithm of the ratio of local diversity to dark diversity (PARTEL, SZAVA-KOVATS & ZOBEL, 2013). Community completeness is mainly related to local contemporary processes including biotic interactions and local-scale dispersal limitation (PARTEL *et al.*, 2016). Macroscale variation in dark diversity often reflects variation in species pool sizes (ZOBEL, 1997; PARTEL, SZAVA-KOVATS & ZOBEL, 2011) due to changes in abiotic conditions, limited dispersion and/or low competitive ability (RIIBAK *et al.*, 2015), and both are, thus, often related to macroscale environmental variables, such as climate and soil fertility. Processes

shaping ecological communities (e.g., dispersal and biotic interactions) vary among regions and habitat types because of differences in species, environmental conditions, climate, and land use (LENOIR *et al.*, 2010). However, the impacts of climate-soil-disturbance are largely unknown on shaping the patterns of dark diversity and completeness in seasonally dry tropical forests (SDTF).

There is a pressing need to fill this knowledge gap SDTF are under intense disturbance effects, mainly deforestation (MALHI *et al.*, 2014; ALLEN *et al.*, 2017; RITO *et al.*, 2017). FAHRIG *et al.* (2003, 2013, 2017, 2019, 2021) and WATLING *et al.* (2020) argues that species richness in plots of fixed size is more strongly and positively related to the amount of habitat around the plot than to patch size or isolation. Smaller and more isolated patches have lower species richness than larger and less isolated ones (MACARTHUR & WILSON, 1967; HAILA, 2002; LAURANCE, 2008) and species richness in a fixed-size plot increases with the total area of habitat in the "local landscape" around the plot (FAHRIG, 2013; WATLING *et al.*, 2020). However, most SDTFs historically support low-income rural populations widely dependent on forest resources for proper livelihood, such as fodder, firewood and timber (SINGH, 1998; DAVIDAR *et al.*, 2010; RIBEIRO *et al.*, 2015). Such a frequent and continuous removal of small portions of forest biomass is known as "chronic anthropogenic disturbance" (CAD) (SINGH, 1998; ANTONGIOVANNI *et al.*, 2020) can decrease plant species diversity (REDFORD, 1992; LEAL, ANDERSEN & LEAL, 2014; RIBEIRO *et al.*, 2015, 2016, 2019). However, the relative importance of deforestation and CAD on plant diversity is still on debate in SDTF vegetation (RIBEIRO *et al.*, 2015, 2016; RITO *et al.*, 2017; SFAIR *et al.*, 2018).

Besides deforestation and CAD, STDFs are one of the most threatened ecosystems by climate extremes (MORO *et al.*, 2015). SDTF can be associated with low levels of rainfall and high temperatures with strong seasonal drought (MAIA *et al.*, 2020) on fertile soils with a moderate to high pH (MURPHY & LUGO, 1986; PENNINGTON *et al.*, 2009; LE BAGOUSSE-PINGUET *et al.*, 2017). Existing evidence indicates that variations in plant diversity are driven by rainfall and temperature (ESQUIVEL-MUELBERT *et al.* 2017; MAIA *et al.*, 2020) because physiological mechanisms, such as photosynthesis, are dependent of water and temperature (PORTILLO-QUINTERO *et al.*, 2015; MARKS, MULLER-LANDAU & TILMAN, 2016; ESQUIVEL-MUELBERT *et al.*, 2017). By influencing ecological processes with conditions and resources at various scales (e.g., climate, topography), the soil attributes have direct consequences on plant communities being an important factor for tropical forests

diversity patterns on SDTFs (VLEMINCKX *et al.*, 2015; KRISHNADAS *et al.*, 2016; De SOUZA *et al.*, 2019).

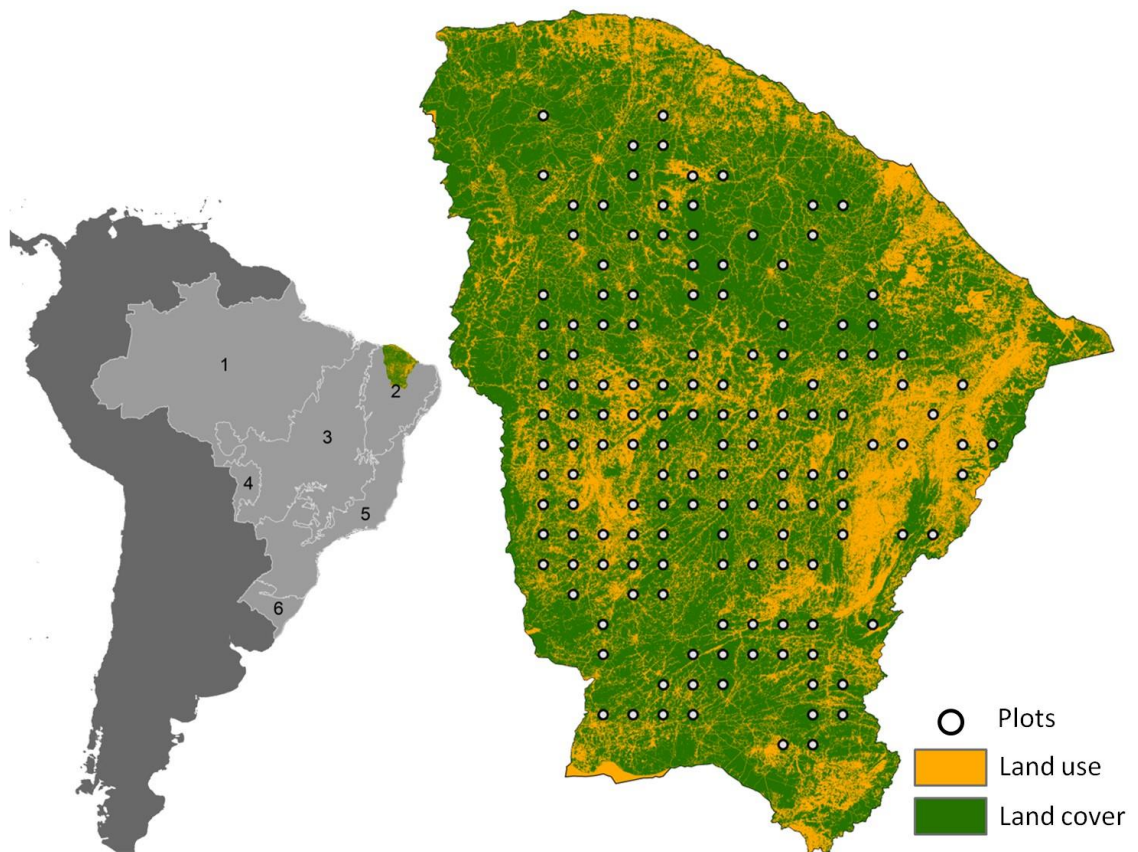
One of the largest areas of SDTF is the Caatinga in the northeast of Brazil, with over 800,000 km² (SAMPAIO, 1995; MILES *et al.*, 2006). Nearly half of the vegetation cover was lost due to human occupation and the remaining habitat is under intense human pressure (ANTONGIOVANNI, VENTICINQUE & FONSECA, 2018) by slash-and-burn agriculture, logging and fuelwood extraction, causing both forest loss and degradation (SILVA *et al.*, 2017; MELO, 2017). Furthermore, easy access to Caatinga remnant areas has also been described as a key factor in the over-exploitation of woody plants for coal, civil construction industry and domestic use (GARIGLIO *et al.*, 2010). The seasonality and rainfall distribution, associated with elevated temperatures and highly variable edaphic conditions, drive a diverse spectrum of Caatinga formations (MORO *et al.*, 2014, 2015) from open areas with shrub and herbaceous vegetation, to areas where tree species predominate in both species' richness, such as arboreal Caatingas (*sensu* GRAEFF, 2015).

Aiming to understand how the relative importance of natural and anthropogenic factors affect not only species richness but also dark diversity, completeness and species pool richness patterns of different life-forms: trees, shrubs, herbs and vines, we tested the hypothesis that plant diversity increases with larger patches, less isolated patches landscapes surrounded by more habitat, with lower chronic anthropogenic disturbance, wetter and hotter climate, and higher soil fertility. Therefore, we ask if: 1. the environmental and disturbance variables influence the diversity of plants and their different life forms in the Caatinga of Ceará? 2. Dark diversity, completeness and species pool richness respond differently compared to observed diversity?

10 MATERIAL AND METHODS

10.1 Study area

The study was carried out in Seasonally Dry Tropical Forests (*sensu* PENNINGTON *et al.*, 2009), named locally as Caatinga, in Ceará state (Figure 4). In general, the Caatinga from Ceará has annual mean temperatures nearly 25 °C and annual precipitation ranging from 240 to 1500 mm (PRADO, 2003; SAMPAIO, 1995). The soils are shallow, stony and rich in nutrients (SAMPALIO, 1995; De QUEIROZ *et al.*, 2017), and when the rainy season ends, edaphic water does not last very long (De QUEIROZ *et al.*, 2017). The vegetation in deciduous and spiny woodlands or small forests mostly growing on exposed crystalline rock terrains of the Sertaneja Depression. Woody plants are composed mostly of highly branched, deciduous small trees, shrubs, many with spines, and herbs that are mostly annual herbs (LEAL *et al.*, 2005; PENNINGTON *et al.*, 2009; De QUEIROZ *et al.*, 2017). The Caatinga is one of the richest floras among the Seasonally Dry Tropical Forests (PENNINGTON *et al.*, 2009) which are partially determined by the aridity gradient (SILVA & SOUZA, 2018).



10.1.1 Figure 4. Locations of 144 plots (white points) installed on the Caatinga on the crystalline landscapes the Sertaneja Depression of Ceará State. The map is a derived from a classified raster dataset. The dark green color indicates original Caatinga vegetation on crystalline formations (habitat; land cover) and yellow (non-habitat; land use: agriculture, mines, villages, crops, agriculture and pasture mosaic).

10.2 Sampling design

We used the IFN (“Inventário Florestal Nacional”) database provided by the Brazilian Forest Service (“Serviço Florestal Brasileiro”; SFB, 2019), which comprises 376 grids of 20 km x 20 km (conglomerate) distant at least 20 Km from each other (Figure 4). Of the 376 points, 232 points were excluded for our analysis, because they were in tropical moist forest, savanna or coast vegetation: we considered only the Caatinga vegetation which is a deciduous spiny forest located in crystalline lowlands, i.e., 144 plots specific to the Caatinga according (MORO, MACEDO & MOURA-FÉ, 2015) and classification based to MapBiomias (MAPBIOMAS, 2019). Starting in October 2013 and finishing in August 2014, a conglomerate was installed with four sample subunits with 20 x 50m each, representing a total area of 4,000 m². However, what we did was add the values of the conglomerate axes (200 x 200m) as the smallest sample

unit or plot, representing a total area of 40,000 m², so that all data could be overlapping to that square area. In each subunit, data on the existing vegetation were collected, such as the diameter and total height of the trees, cacti and palms, with diameter at breast height (DAP) greater than or equal to 10 cm. It is important to highlight that most woody plants in Caatinga have DAP \leq 10cm (SFB, 2019). For this reason, in each four subunits, a smaller plot (10m x 10m) was used to measure shrubs and trees with a DAP between 5 and 10 cm, herbs and vines (without secondary growth; **Supplementary Material 1**). Because many species were not sampled by the IFN, 68 plots of trees, 48 of shrubs, 44 of herbs and 113 of vines had zero species. A total of 2,148 botanical samples of trees, shrubs, herbs and vines species were collected and sent to the “Herbário Prisco Bezerra” of the Federal University of Ceará (UFC) to identify the species with assistance from specialists following the Flora e Fungi do Brasil (CARVALHO, 2022). The IFN data used in the analyzes are composed of exotic and native species. We counted 466 native species for the different plant life-forms for this study and the analyzes were performed for these databases.

10.3 Climate data

Because the Caatinga is a semi-arid region, we considered climatic variables related to temperature and precipitation as potentially significant ecological drivers of species richness. For each site we extracted the 19 bioclimatic variables from the “Climatologies at high resolution for the earth’s land surface areas”. The climate data was used in the station interpolation algorithm of the respective dataset consist of a monthly temperature and precipitation climatology for the years 1979–2013 (KARGER *et al.*, 2017). We considered the uncorrelated variables (**Supplementary Material 2**): annual mean temperature [$^{\circ}\text{C} \cdot 10$], annual precipitation [mm/year] and precipitation of driest quarter [mm/quarter].

10.4 Soil data

Soil data were collected by IFN in each plot within a radius of up to 2 meters from the central point of each conglomerate, with samples at a depth of 0-20 cm, using Dutch auger or digger and were collected and stored in resistant plastic bags and sent to a specialized laboratory for analysis. From 15 chemical and physical variables we considered the uncorrelated ones (**Supplementary Material 2**): phosphorus ($\text{mg} \cdot \text{kg}^{-1}$), base saturation index (%) and clay

content (g.kg^{-1}) because they are directly related to soil fertility (LU *et al.*, 2002; SANTOS *et al.*, 2012).

For more details about soil sampling, see the National Forest Inventory Field Manual and forms, available at: <http://www.florestal.gov.br/documentos/informacoes-florestais/inventario-florestal-nacional-ifn/documentos>.

10.5 Remote-sensed habitat classification and pre-processing data

Mapping land use and land cover require regular updates and high spatial resolution data to better understand the historical land use and land cover dynamics, and the subsequent impacts on the country's biomes (PONTIUS & MILLONES, 2011; FONSECA *et al.*, 2017; SOUZA Jr *et al.*, 2020). We considered the limits of the Caatinga under crystalline lowlands from the phytocological units mapped by MORO, MACEDO & MOURA-FÉ (2015) using the Qgis dissolve tool (QGIS, 2021). The crystalline Caatinga map (MORO, MACEDO & MOURA-FÉ, 2015) was used as a mask layer to cut the Mapbiomas land use and land cover data.

Then, we used georeferenced digital files containing data on vegetation remnants for 2014 according Mapbiomas, with the best updated and accurate image (accuracy = 81.8%) in the last collection published (MAPBIOMAS 5.0, 2019) adjusting the date of the satellite image to the end of 2014, coinciding with the forest inventory in the state of Ceará (SFB, 2019). The Mapbiomas raster and the map for the Caatinga under crystalline using the shapefile by MORO, MACEDO & MOURA-FÉ (2015) was reclassified to create a new raster with habitat (only Caatinga vegetation) and non-habitat using the dissolve layers (union) tool in Qgis (OLSON *et al.*, 2001; MORO, MACEDO & MOURA-FÉ, 2015). The values in the new raster were applied using a defined range of values in pixel classes. The non-habitat category included several land uses, such as pasture (1,924,517.82 ha, 39.57%), agriculture (497,305.69 ha, 10.22%), agriculture and pasture mosaic (1,642,524.19, 33.77%), temporary crops (217,739.72 ha, 4.48%), urban infrastructure (81,540.90 ha, 1.68%), mining (268.80 ha, 0.005%), perennial crop (279,565.96 ha, 5.75%), soy beans (1.43 ha, 0.00003%), other temporary crops (217,738.30 ha, 4.48%) and other non-vegetated areas (2,853.32 ha, 0.06%) (MAPBIOMAS, 2019; SOUZA Jr *et al.*, 2020).

Additionally, the shapefile composed of a layer paved (provided by DNIT – “*Departamento Nacional de Infraestruturas de Transportes*”; <http://servicos.dnit.gov.br/vgeo>) and unpaved (provided by OSM – *OpenStreetMap*; <http://www.openstreetmap.org/>) roads (IBGE, 2010) were superimposed on the shapefile of the forest remnants to obtain a more accurate scenario of the habitat amount pattern of the Caatinga, since Mapbiomas does not consider roads in their classification. An extension of 110 m for each side of the paved roads and 60 m for each side of the unpaved roads was arbitrarily considered as a deforested area and subtracted from the original forest area (ANTONGIOVANNI *et al.*, 2018).

10.6 Deforestation variables

The cell size of satellite images used to create forest cover maps was 30x30m² (MAPBIOMAS, 2019). A measure of the habitat amount, patch size (the patch in which a sample plot is located) (WATLING *et al.*, 2020) and isolation with distance-based (PRUGH, 2009) on nearest-neighbour distance effects were estimated for the entire Caatinga landscape in Ceará based on FAHRIG (2013, 2017). We used the “class level metric” in landscape metrics package (HESELBARTH *et al.*, 2019) in R (R CORE TEAM 2019) that returns one value for habitat (Caatinga) and non-habitat (non-Caatinga) in the landscape. The habitat amount is the sum of the area of all patches belonging to Caatinga vegetation (MCGARIGAL, CUSHMAN, & ENE, 2012). The habitat amount was calculated as the percentage of caatinga vegetation in a predetermined six buffers area around the plot: 1, 2, 3, 4, 5 and 6 with 1, 2, 3, 4, 5 and 6 Km of radii. The buffer with the highest R² for each response variable was used in the complete generalized linear model because it has the greatest effect of landscape habitat amount.

The patch size data was obtained by measuring the area of patch that contains the plot and isolation was calculated on the basis the nearest-neighbors mean distance of the focal patch to three other patches in the local landscape (FAHRIG, 2013; WATLING *et al.*, 2020). The metrics habitat amount, patch size and isolation effects described are not correlated with each other (**Supplementary Material 2**) and were obtained use the landscape metrics package (HESELBARTH *et al.*, 2019) in R (R CORE TEAM 2019).

10.7 Chronic anthropogenic disturbance (CAD)

We used the CAD calculated by ANTONGIOVANNI *et al.* (2020) that was estimated using 14 variables, such as human population, infrastructure, grazing, logging and fire (vectors). The variables were carefully selected from a large array of official variables available from Brazilian governmental sources (e.g., IBGE, MMA) to capture relevant, independent dimensions of each vector. A correlation matrix among the 14 variables demonstrated that 96.8% of the 91 estimated correlations were lower than 0.4, supporting their relative independence. All data is available in the Dryad Digital Repository (ANTONGIOVANNI *et al.*, 2020).

The analyzed variables, expressed as distance or density, were used to generate 14 primary surfaces of disturbance along the whole Caatinga territory, each pixel receiving a value corresponding to its disturbance intensity. Therefore, the CAD index data was calculated for each pixel as the weighed sum of the 14 primary variables (d_i , $0 \leq d_i \leq 100$) considering their relative importance (w_i , $0 \leq w_i \leq 1$), standardized by the maximal weighted sum (mws) recorded for a pixel in the whole landscape, including the anthropogenic matrix (ANTONGIOVANNI *et al.*, 2020). Thus, $CAD\ index = \sum d_i \cdot w_i / mws$ ($1 \geq CDI \geq 0$) where values close to one indicate most disturbed pixel, whereas values close to zero, least disturbed pixel. We used the data published by ANTONGIOVANNI *et al.* (2020) and, for those plots that had no data, we took the closest point to the CAD value index for the Ceará state.

10.8 Estimation of dark diversity, community completeness and species pool

To obtain the best possible estimates of observed and dark diversity, we used Beals probability index (BEALS, 1984), as recommended by MUNZBERGOVÁ & HERBEN (2004) and LEWIS, SZAVA-KOVATS & PARTEL (2016). This index can be used to estimate the probability of a species occurring in a particular region based on its co-occurrence within other regions and was calculated using the package “vegan” (OKSANEN *et al.*, 2016) and “DarkDiv” (PARTEL *et al.*, 2019) in R. The probability of occurrence for all species in dark diversity was defined by 0.7, that is, 70% or more chance of being in dark diversity for each specie. For each area, a species was included in the dark diversity when it was absent from a target plot and its occurrence probability was higher than its threshold value (0.7). The regional pool was

calculated between the sum of observed diversity and dark diversity (PARTEL *et al.*, 2011) and it includes all the species present in a particular area without regard to the specific ecological conditions at the target site. This is generally easy to measure when regional lists of flora or species occurrence maps are available. In addition, it was calculated the community completeness for each region using $\log(\text{observed richness}/\text{dark diversity})$. Positive value means high observed diversity and low dark diversity, whereas negative values indicate high dark diversity. Community completeness determine how much of the species pool was realized within a local community (PARTEL, SZAVA-KOVATS & ZOBEL, 2013).

10.9 Data analysis

We tested for spatial correlation with Mantel tests between Bray-Curtis's dissimilarity for species assemblage and the Euclidean distance between plots (**Supplementary material 3**). We used general linear models (GLMs) with response variables: plant richness, dark diversity, completeness and species pool. For predictor variables we use annual mean temperature, annual mean precipitation and precipitation of driest quarter for climate, base saturation index, assimilable phosphorus and clay content, for soil and acute (habitat amount, fragment size, isolation) and chronic (CAD) disturbances. The response and predictor variables were z-transformed to put the axes on the same scale. For explanatory variables in a set of generalized linear models (GLMs) we use Poisson distribution corrected by over dispersed data for species pool, dark diversity and plant richness, and Gaussian distribution for completeness. Additionally, we calculated the generalized linear models correcting for spatial correlation (Generalized Least Square), but the results were very similar to the GLM. Therefore, we show the GLMs results. All analyses were performed in R version 4.4.1 (R CORE TEAM, 2019) using the package “visreg” (BREHENY & BURCHETT, 2017) for general linear model's graphs, “corrplot” (WEI & SIMKO, 2021) for the correlation tables.

11 RESULTS

The observed number of species, dark diversity, completeness and species pool size metrics were highly correlated among them ($r > 0.7$ e $r < -0.7$) (**Supplementary Material 4**).

In general, soil variables are poor predictors of species diversity (**Supplementary Material 5**), whereas habitat amount and rainfall are more prone to be related to species diversity (Table 2; Figure 5). Areas with higher rainfall in the driest months tend to have higher

observed diversity of plants (all life forms together) and shrubs, whereas areas with higher mean annual rainfall tend to have higher observed diversity of trees and lower of herbs. Areas with higher temperature and mean annual rainfall tend to have higher dark diversity of all life forms together and trees, whereas precipitation of driest quarter are more prone to be related to completeness of all life forms, shrubs and herbs. However, higher temperature tends to have lower completeness of shrubs. Higher diversity of species pool of all plants together, trees and herbs tend to occur in areas with higher rainfall, as well as in areas with higher temperature for trees (Table 2; Figure 5).

Concerning acute disturbance, habitat amount and isolation is more prone to be related to species diversity, dark diversity and species pool than completeness: only patch isolation was positively related to the completeness of herbs (Table 2; Figure 5). Areas with more habitat tend to have higher diversity, dark diversity, completeness and species pool of vines. Chronic anthropogenic disturbance was only positively related to completeness of trees (Table 2; Fig. 5)

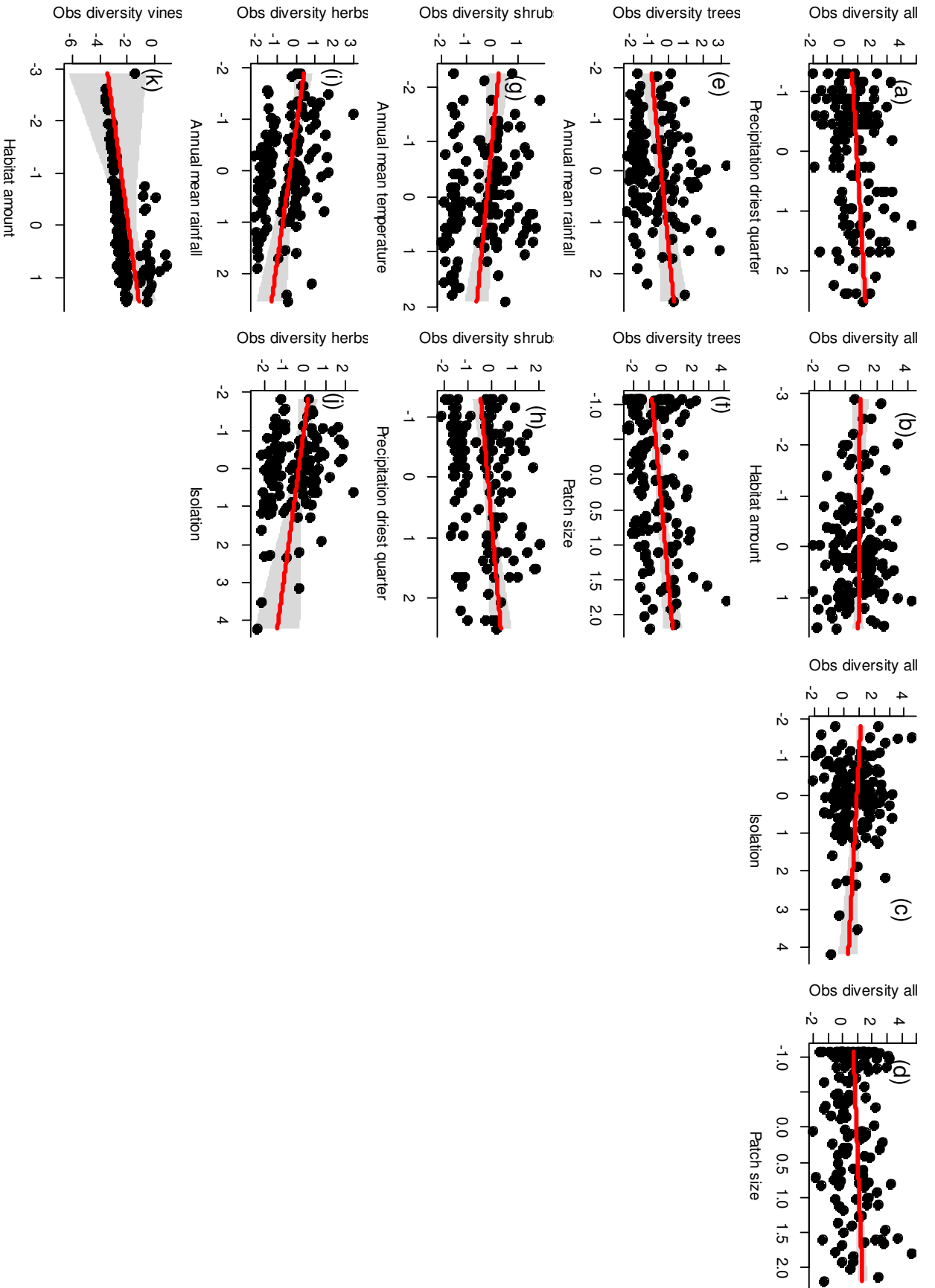
11.1 Table 2. Regression of general linear models of observed, dark diversity, completeness and species pool for all plant dataset and different plant life-forms using variable of climate, soil, chronic and acute disturbance.

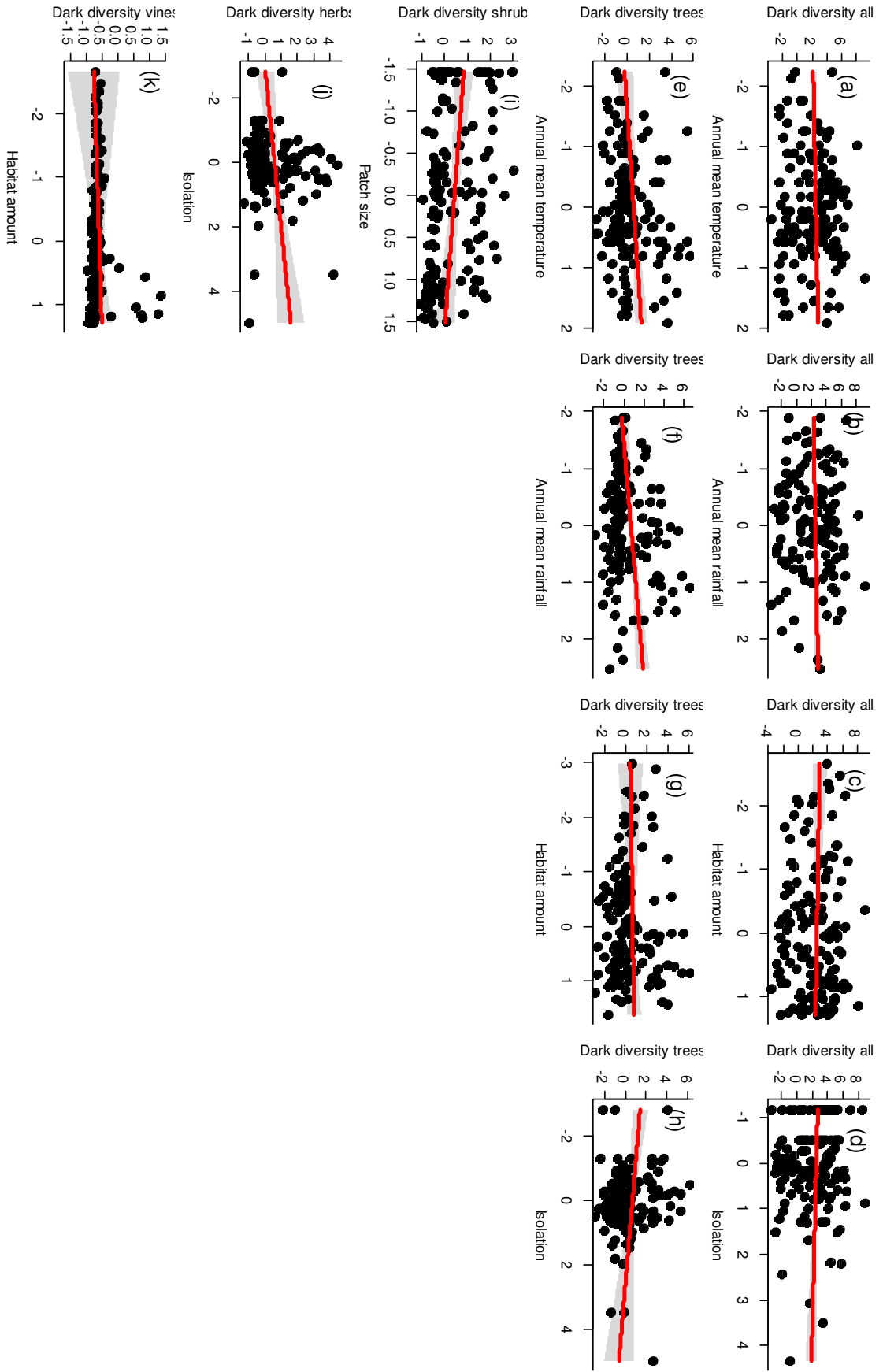
Plant life forms	Variables	Observed diversity		Dark diversity		Completeness		Species pool		Df
		Estimate	F value	Estimate	F value	Estimate	F value	Estimate	F value	
All forms	Annual mean temperature	0.03	0.07	0.16	4.21 *	-0.10	0.48	0.13	3.80	142
All forms	Annual mean rainfall	-0.01	3.07	0.13	5.81 *	-0.25	1.24	0.10	6.75 *	141
All forms	Precipitation of driest quarter	0.23	8.10 **	0.00	0.20	0.46	9.09 **	0.04	0.02	140
All forms	Clay content	-0.04	0.61	-0.01	0.19	-0.03	0.00	-0.02	0.33	139
All forms	Assimilable phosphorus	0.01	0.49	-0.04	0.00	0.12	0.26	-0.03	0.04	138
All forms	Base saturation index	0.10	0.53	0.03	0.29	0.01	0.25	0.04	0.45	137
All forms	Chronic anthropogenic disturbance	0.00	0.85	-0.04	0.03	0.08	0.36	-0.04	0.01	136
All forms	Habitat amount	-0.02	4.79 *	-0.14	4.45 *	-0.32	0.27	-0.15	5.92 *	135
All forms	Isolation	-0.13	3.95 *	-0.14	4.81 *	0.40	6.15 *	-0.13	5.53 *	134
All forms	Patch size	0.19	5.36 *	0.24	1.85	0.45	1.54	0.26	2.83	133
Multiple R²		0.17		0.13		0.13		0.14		
Trees	Annual mean temperature	0.23	3.61	0.36	10.60 **	-0.18	0.03	0.32	9.69 **	142
Trees	Annual mean rainfall	0.28	11.53 ***	0.47	26.14***	-0.06	0.55	0.42	25.12 ***	141
Trees	Precipitation of driest quarter	0.26	2.16	0.16	0.48	0.38	0.31	0.17	0.92	140
Trees	Clay content	-0.00	0.32	-0.18	1.68	-0.31	1.65	-0.13	1.40	139
Trees	Assimilable phosphorus	-0.16	0.05	0.03	0.30	-0.11	0.16	-0.01	0.13	138
Trees	Base saturation index	0.18	1.27	0.15	1.72	0.28	0.97	0.15	1.85	137
Trees	Chronic anthropogenic disturbance	0.03	1.36	-0.09	1.62	0.67	4.17 *	-0.09	1.98	136
Trees	Habitat amount	-0.06	3.44	0.07	5.19 *	0.03	0.92	0.06	5.98 *	135
Trees	Isolation	-0.12	1.33	-0.25	4.83 *	0.25	0.67	-0.20	3.96 *	134
Trees	Patch size	0.41	7.50 **	0.13	0.65	0.58	2.87	0.17	1.27	133
Multiple R²		0.20		0.33		0.09		0.31		

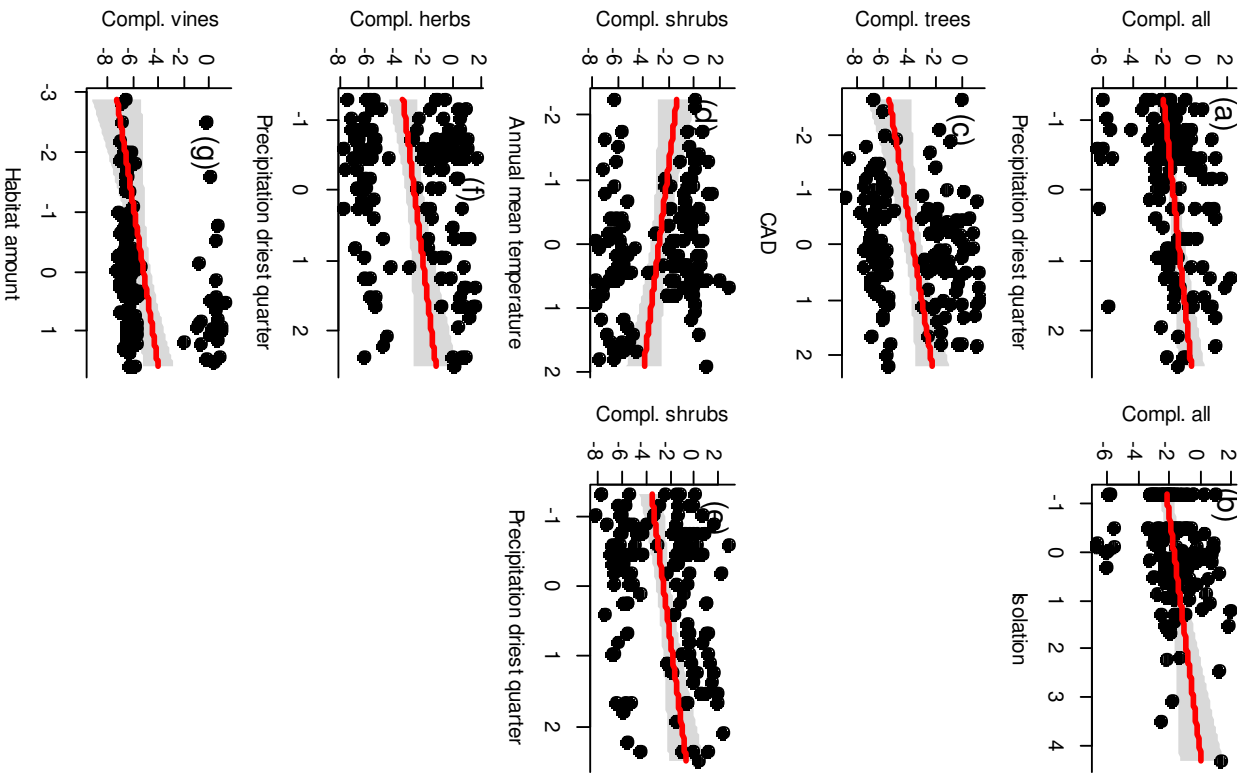
Shrubs	Annual mean temperature	-0.20	6.32 *	-0.05	0.15	-0.62	7.29 **	-0.11	2.18	142
Shrubs	Annual mean rainfall	-0.00	2.19	-0.01	0.01	-0.21	0.23	-0.00	0.42	141
Shrubs	Precipitation of driest quarter	0.22	5.73 *	-0.13	2.19	0.76	8.76 **	0.00	0.03	140
Shrubs	Clay content	-0.09	0.25	-0.06	0.30	-0.13	0.00	-0.07	0.35	139
Shrubs	Assimilable phosphorus	0.13	1.09	0.13	0.60	0.37	1.52	0.13	1.06	138
Shrubs	Base saturation index	-0.10	1.89	-0.05	1.07	-0.06	0.14	-0.07	1.70	137
Shrubs	Chronic anthropogenic disturbance	-0.00	0.00	0.18	3.52	-0.15	0.48	0.10	1.59	136
Shrubs	Habitat amount	0.08	2.61	0.18	0.05	0.02	1.20	0.13	0.27	135
Shrubs	Isolation	0.09	0.93	-0.09	1.01	-0.05	3.11	-0.09	1.26	134
Shrubs	Patch size	0.05	0.10	-0.27	3.92 *	0.01	0.17	-0.14	1.31	133
Multiple R²		0.13		0.10		0.15		0.07		
Herbs	Annual mean temperature	0.16	1.29	0.10	0.15	0.16	0.17	0.12	0.52	142
Herbs	Annual mean rainfall	-0.38	6.21 *	-0.24	2.52	-0.68	1.12	-0.27	4.56 *	141
Herbs	Precipitation of driest quarter	0.23	3.27	-0.04	0.30	0.61	4.60 *	0.04	0.06	140
Herbs	Clay content	-0.05	0.30	-0.11	0.08	0.05	0.14	-0.09	0.19	139
Herbs	Assimilable phosphorus	0.08	0.53	0.20	1.35	0.37	1.06	0.15	1.32	138
Herbs	Base saturation index	0.12	0.84	-0.11	1.51	0.38	0.85	-0.03	0.34	137
Herbs	Chronic anthropogenic disturbance	0.00	0.01	0.10	1.32	-0.05	0.10	0.09	1.25	136
Herbs	Habitat amount	-0.11	0.02	0.27	1.07	-0.09	0.28	0.16	0.66	135
Herbs	Isolation	-0.25	4.75 *	0.20	4.90 *	-0.55	2.85	0.18	4.88 *	134
Herbs	Patch size	0.01	0.02	-0.12	0.70	0.00	0.00	-0.04	0.10	133
Multiple R²		0.11		0.12		0.08		0.11		
Vines	Annual mean temperature	-0.13	1.04	-0.05	3.14	0.13	0.15	-0.08	2.58	142
Vines	Annual mean rainfall	-0.26	0.09	-0.04	0.26	-0.39	0.00	-0.09	0.23	141
Vines	Precipitation of driest quarter	0.30	1.40	0.04	0.56	0.20	0.65	0.12	1.50	140
Vines	Clay content	-0.06	0.07	-0.03	0.00	-0.01	0.05	-0.03	0.06	139
Vines	Assimilable phosphorus	0.17	0.73	0.08	2.13	0.20	0.76	0.12	1.77	138
Vines	Base saturation index	0.17	0.18	0.00	0.17	0.21	0.03	0.05	0.04	137

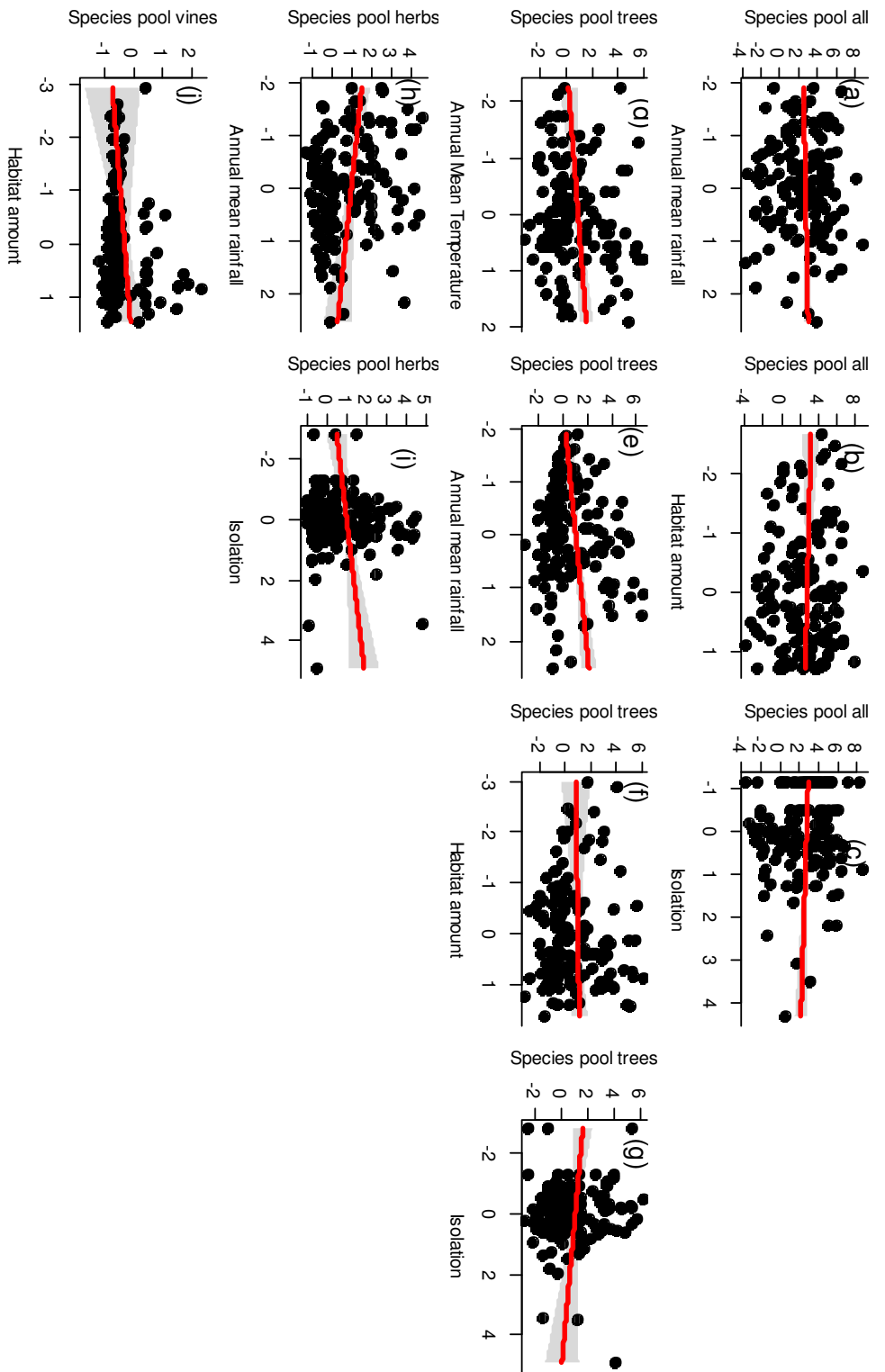
Vines	Chronic anthropogenic disturbance	0.46	2.53	-0.00	0.47	0.00	0.03	0.09	1.63	136
Vines	Habitat amount	0.52	6.51 *	0.06	6.51 *	0.72	9.03 **	0.14	8.54 **	135
Vines	Isolation	-0.07	0.18	-0.06	1.48	0.00	0.00	-0.02	0.14	134
Vines	Patch size	0.10	0.07	0.05	0.16	0.07	0.06	0.11	0.69	133
Multiple R²		0.13		0.14		0.08		0.15		

Note: Explanatory variables are framed according to climate, soil, chronic and acute disturbance variables for all plant dataset and different plant life-forms. We use ordinary least squares with Quasipoisson distribution for observed, dark diversity and species pool, and Gaussian for completeness. R^2 is calculated as $1 - (\text{model deviance}/\text{model null deviance})$ for all response variables. We present the estimate, F value test ($P < 0.05$) and degrees of freedom (Df).









11.2 Figure 5. Parameter estimates with 95% confidence intervals from the significant environmental variables predicting observed diversity, dark diversity, completeness and species pool for all plant dataset and different plant life-forms. Relationships between the all-plants observed diversity and (a) precipitation of driest quarter, (b) habitat amount, (c) isolation and (d) patch size. Relationships between the trees observed diversity and (e) annual mean rainfall and, (f) patch size. Relationships between the shrubs observed diversity and (g) annual mean temperature and, (h) precipitation driest quarter. Relationships between the herbs observed diversity and (i) annual mean rainfall and, (j) isolation. Relationships between the vines observed diversity and (k) habitat amount. Relationships between the all-plants dark diversity and (a) annual mean temperature, (b) annual mean rainfall, (c) habitat amount and (d) isolation. Relationships between the trees dark diversity and (e) annual mean temperature, (f) annual mean rainfall, (g) habitat amount and, (h) isolation. Relationships between the shrubs, herbs and vines dark diversity and (i) patch size, (j) isolation and, (k) habitat amount, respectively. Relationships between the all-plants completeness and (a) precipitation of driest quarter, and (b) isolation. Relationships between the trees completeness and (c) chronic anthropogenic disturbance. Relationships between the shrubs completeness and (d) annual mean temperature, and (e) precipitation driest quarter. Relationships between the herbs completeness and (f) precipitation driest quarter. Relationships between the vines completeness and (g) habitat amount. Relationships between the all-plants species pool and (a) annual mean rainfall, (b) habitat amount, and (c) isolation. Relationships between the trees species pool and (d) annual mean temperature, (e) annual mean rainfall, (f) habitat amount and, (g) isolation. Relationships between the herbs species pool and (h) annual mean rainfall, and (i) isolation. Relationships between the vines species pool and (j) habitat amount.

12 DISCUSSION

Our study addresses the effect of local abiotic conditions (climate, soil, chronic and acute disturbance variables) in shaping communities of vascular plants in Caatinga and shows that, in general, rainfall and habitat amount best explain observed and dark diversity. Our results not only confirm that abiotic conditions are one of the most important factors affecting plant community assembly (ZOBEL *et al.*, 2011), but also shows the importance of habitat amount structuring plant communities, mainly observed diversity. In contrary to other studies (e.g., MORO *et al.*, 2015; RIBEIRO *et al.*, 2015; RITO *et al.*, 2017; MAIA *et al.*, 2020), we found that soil and chronic anthropogenic disturbance are poor predictors of species diversity, for all plant lifeforms. However, the different metrics of species diversity and the life-forms also tend to respond differently to environmental variables. For instance, whereas the richness of trees tends to be higher in wetter, herbs tend to be richer in drier areas. These results highlight the importance to calculate different metrics of species richness and consider different groups of plant communities.

Habitat amount is important for observed plant richness, indicating that large patches probably promote the coexistence of plant species and decrease dark diversity. Interestingly, a high species diversity for vines was found in larger patches, although some studies show that vines are favored by disturbance and, thus, are more abundant in small patches and edge of forest fragments (LAURANCE *et al.*, 2001; CAMPBELL *et al.*, 2018). On the other hand, vines in the Caatinga have shallow roots and low resistance to cavitation (CARVALHO *et al.*, 2016) and could be less favored by disturbance than vines from wetter forests. Therefore, dry season probably has a minor effect on the vine diversity, whereas more habitat could not only imply on more suitable area for seed germination, but also more host trees for vines (SCHNITZER, 2018).

CAD decrease tree species diversity and structure in a dry portion of Caatinga vegetation (RIBEIRO *et al.*, 2015, 2016; RITO *et al.*, 2017). However, we found a positive effect of CAD on the completeness (positive value means high observed diversity and low dark diversity) for trees, the opposite of expected. Apparently, as more trees and shrubs are removed from the forest stand, representatives of *Rhaphiodon*, *Astraea*, *Merremia*, *Richardia*, *Borreria*, and other disturbance-adapted genera replace those more disturbance-sensitive ones (e.g., *Physostemom*) (VIEIRA *et al.*, 2022). On the other hand, MENEZES *et al.* (2020) found that fewer species are expected in the Caatinga under goat browsing pressure. These results are in accordance with others reporting negative effects of overgrazing on the plant diversity of the Caatinga vegetation (SCHULZ *et al.*, 2016).

Our results show a positive annual rainfall effect on species diversity of trees. Rainfall is strongly related to plant assemblages in the Brazilian Caatinga vegetation, particularly affecting species diversity (MORO *et al.*, 2015; RITO *et al.*, 2017; PINHO *et al.*, 2019; MAIA *et al.*, 2020; ARNAN *et al.*, 2022). Although rainfall positively affect the diversity of trees, the observed and species pool richness of herbs is negatively affected by rainfall. Rainfall favor herbs floristic divergence by increasing a set of genera in drier areas (VIEIRA *et al.*, 2022) probably allowing the occurrence of unique species. With the expected increases in temperature and drought events due to climate change, it is crucial to understand how plant lifeforms and dry environments might be affected by these changes using not only patterns of observed diversity but other diversity predictors.

Habitat amount is important for observed plant richness for all life forms and vines and, isolation is important for all life forms and herbs. Furthermore, patch size is important for observed richness for all plant forms and trees. Deforestation drastically alters the amount of

habitat, causing profound impacts on biodiversity (FAHRIG, 2013; THOMPSON *et al.*, 2017; WATLING *et al.*, 2020). Recently, it has been argued that the amount of habitat in the landscape is the main predictor of biodiversity, whereas the spatial structure of the fragmentation plays a secondary role (FAHRIG 2013, 2017). Our results show that the habitat amount not affects plant diversity strongly than patch size and patch isolation, as proposed by FAHRIG (2013) and WATLING *et al.* (2020). However, we recommend that future research takes into account the habitat fragmentation, that is, a difference in spatial pattern. Our results are in accordance with FAHRIG *et al.* (2019, 2021) that forest loss has large negative effects on biodiversity. Therefore, it is necessary to consider the landscape as a management unit, since the Caatinga is a highly populated region with heavy use and scarce financial resources to promote the conservation of biodiversity and ecosystem services for the long term (ANTONGIOVANNI *et al.*, 2018).

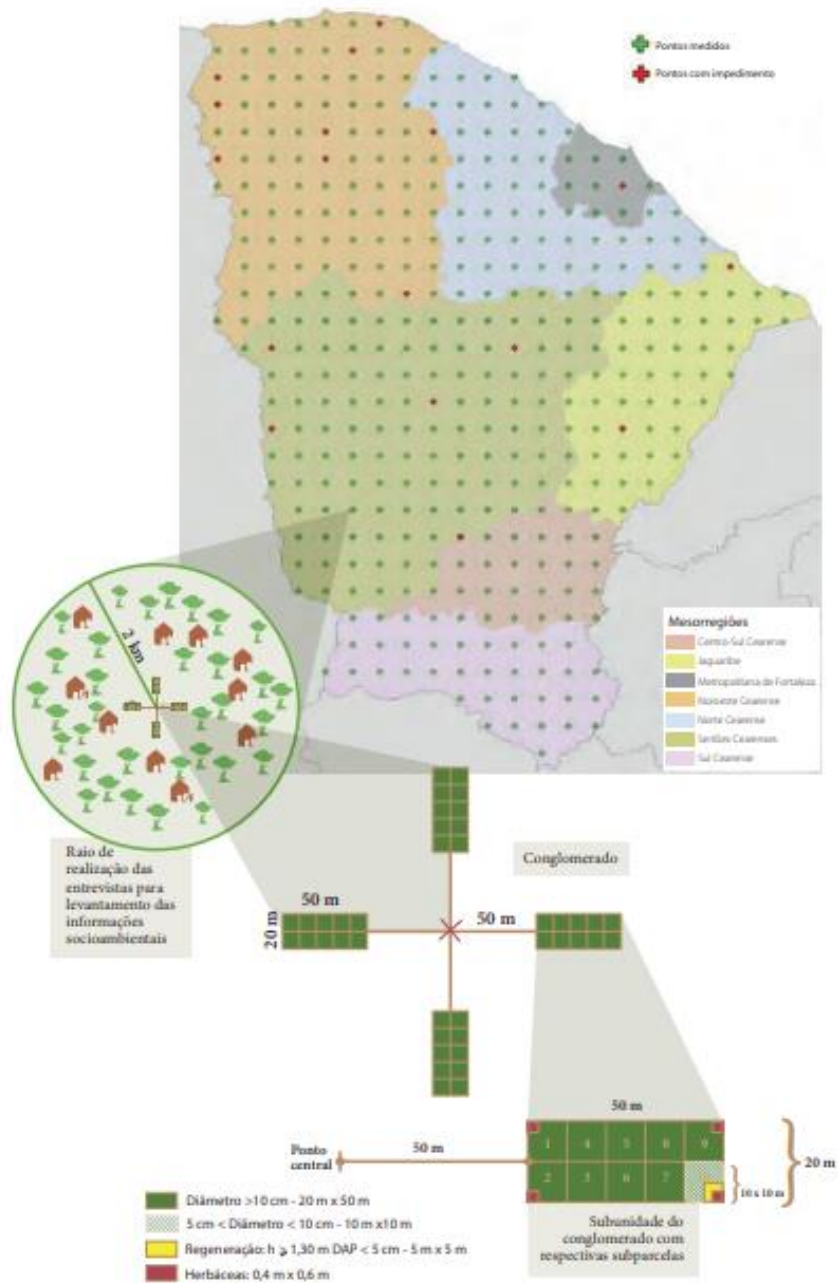
The patterns we have uncovered shed light on the poorly understood interplay between climate, soil, acute and chronic disturbance in plant species in dry forests highlighting the importance of including the missing species set. This study shows that different diversity measures contribute with different aspects to better understand drivers of diversity. For example, the positive effect of rainfall on trees species pool and richness could indicate that rainfall increases trees species richness, whereas the positive effect on dark diversity of trees indicates that fewer species are missing when rainfall is low. Therefore, we should prioritize areas with high observed diversity for the conservation of Caatinga species. However, observed and dark diversity vary independently and high observed diversity do not always mean low dark diversity and vice versa (PARTEL *et al.*, 2011). The concept of dark diversity can complement and improve the robustness of existing approaches in conservation prioritization and management decisions (LEWIS, SZAVA-KOVATS & PARTEL, 2016).

13 CONCLUSION

Dark diversity is a new and useful concept to indicate how many species hidden behind its observed species in a community (PARTEL, SZAVA-KOVATS & ZOBEL, 2011, 2013). With global biodiversity rapidly decreasing, it is vital to understand the drivers of biodiversity to prioritize conservation and make management more efficient. In this study, the climate, habitat amount and patch isolation seem to be the strongest predictor not only of plant richness but also for the dark diversity. Our results strongly emphasize that efforts to conserve and restore Caatinga will require a different metrics of diversity. Therefore, areas that rainfall more and have a large habitat amount should be a priority for conservation, as they present greater observed diversity.

SUPPLEMENTARY MATERIAL CHAPTER 2

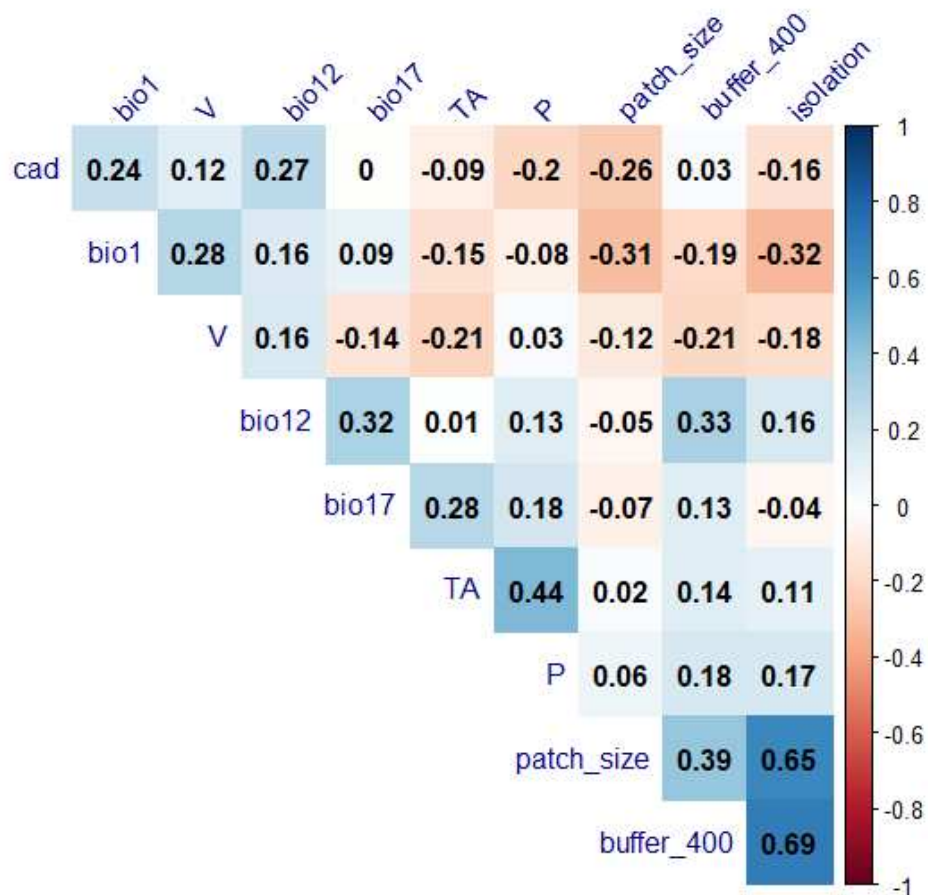
Supplementary Material 1



Supplementary Figure 04. Cear  national forest inventory (IFN) sampling scheme. Conglomerate plots for collecting different plant life forms: trees, shrubs, herbs and vines established by IFN. Access in: <https://dados.gov.br/dataset/ifn-inventario-florestal-nacional>.

Supplementary Material 2

Supplementary Table 06. Correlation between the bio1= annual mean temperature [$^{\circ}\text{C} \cdot 10$], bio12=annual precipitation [mm/year], bio17=precipitation of driest quarter [mm/quarter], assimilable phosphorus (P, $\text{mg} \cdot \text{kg}^{-1}$), base saturation index (V, %), clay content (TA, $\text{g} \cdot \text{kg}^{-1}$), chronic anthropogenic disturbance (cad), habitat amount (buffer_400, ha), isolation (m) and patch size (m).

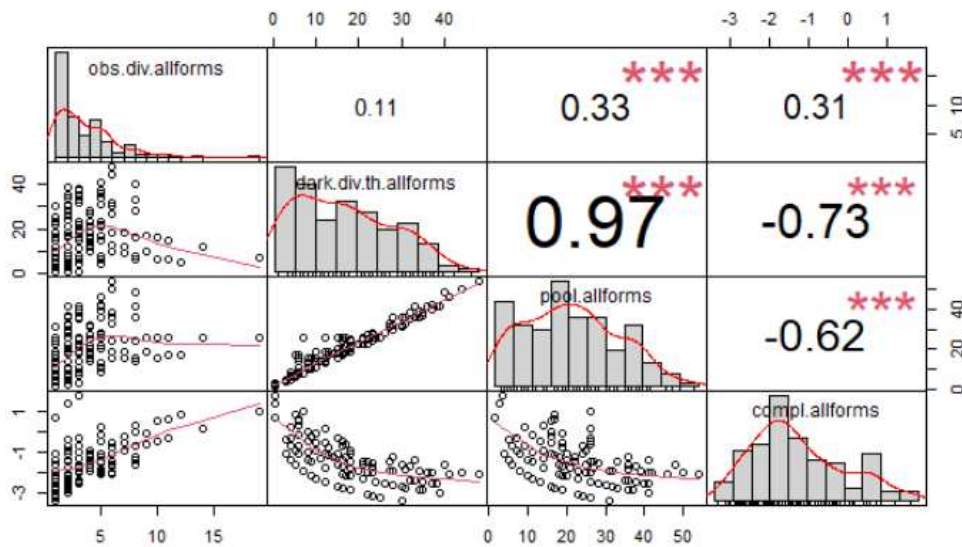


Supplementary Material 3

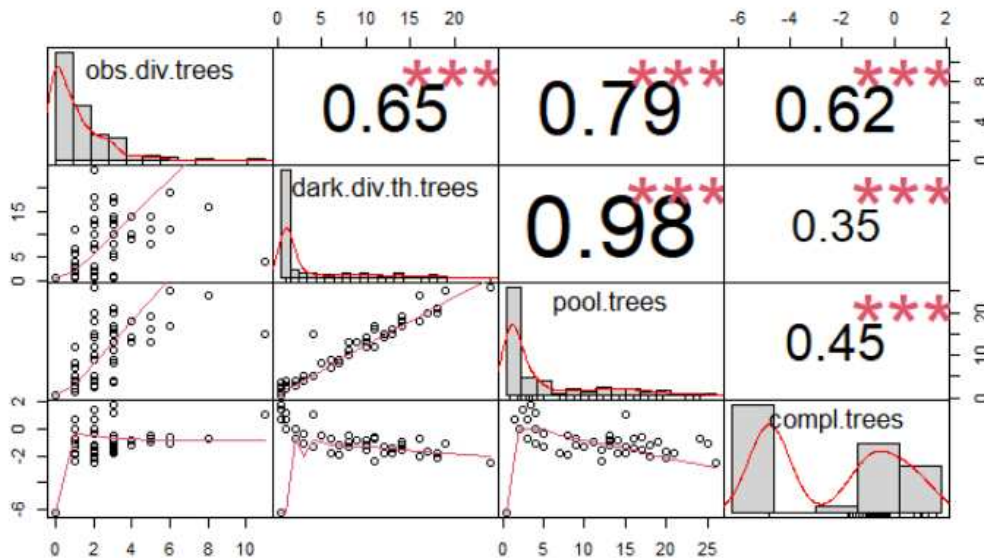
Supplementary Table 03. Regression models tested for spatial autocorrelation with Mantel tests, using bray-curtis dissimilarity. Number of permutations: 999.

	All data	Trees	Shrubs	Herbs	Vines
Mantel statistic r	0.06	0.12	0.01	-0.07	0.02
Significance	0.00	0.00	0.35	0.98	0.34

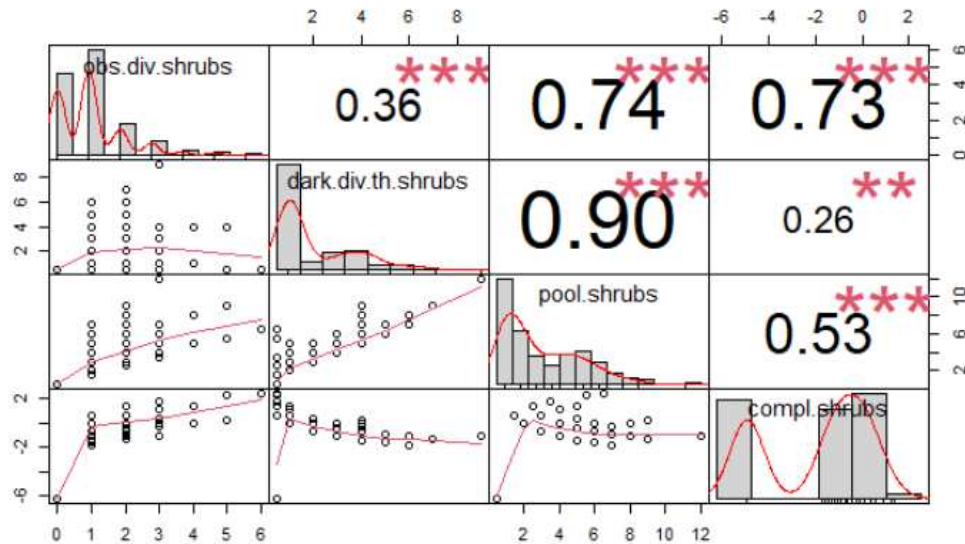
Supplementary Material 4



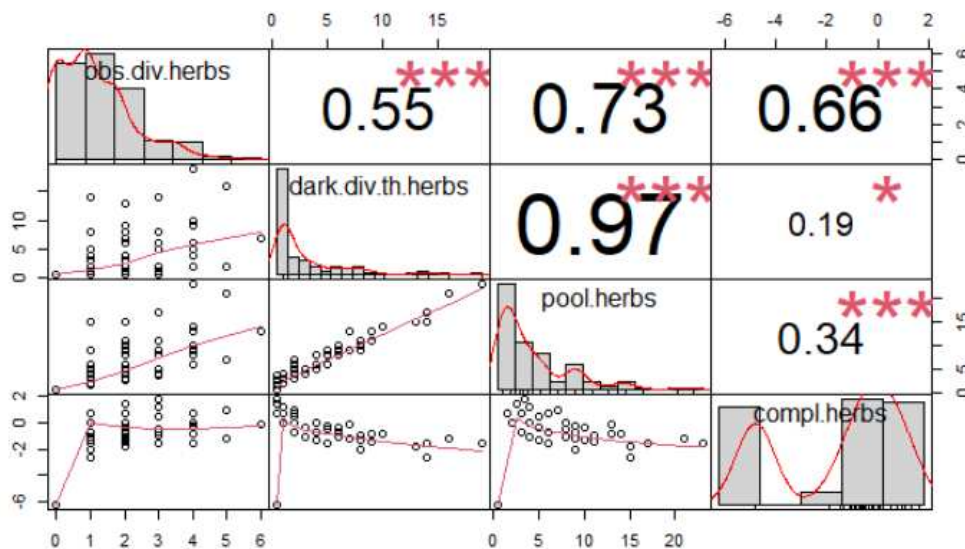
Supplementary Figure 05. Correlation between the observed diversity, dark diversity, completeness and species pool using Spearman rank correlations for all forms data.



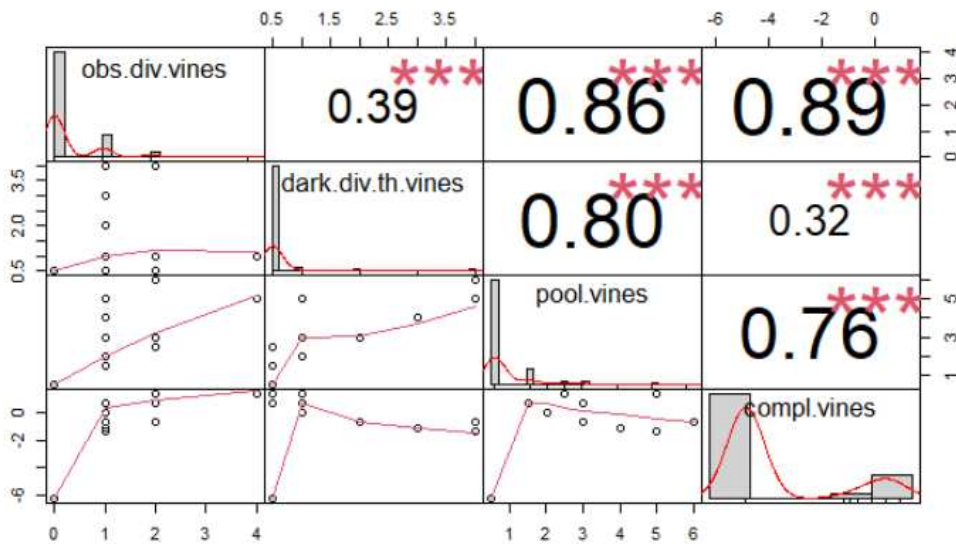
Supplementary Figure 06. Correlation between the observed diversity, dark diversity, completeness and species pool using Spearman rank correlations for trees data.



Supplementary Figure 07. Correlation between the observed diversity, dark diversity, completeness and species pool using Spearman rank correlations for shrubs data.

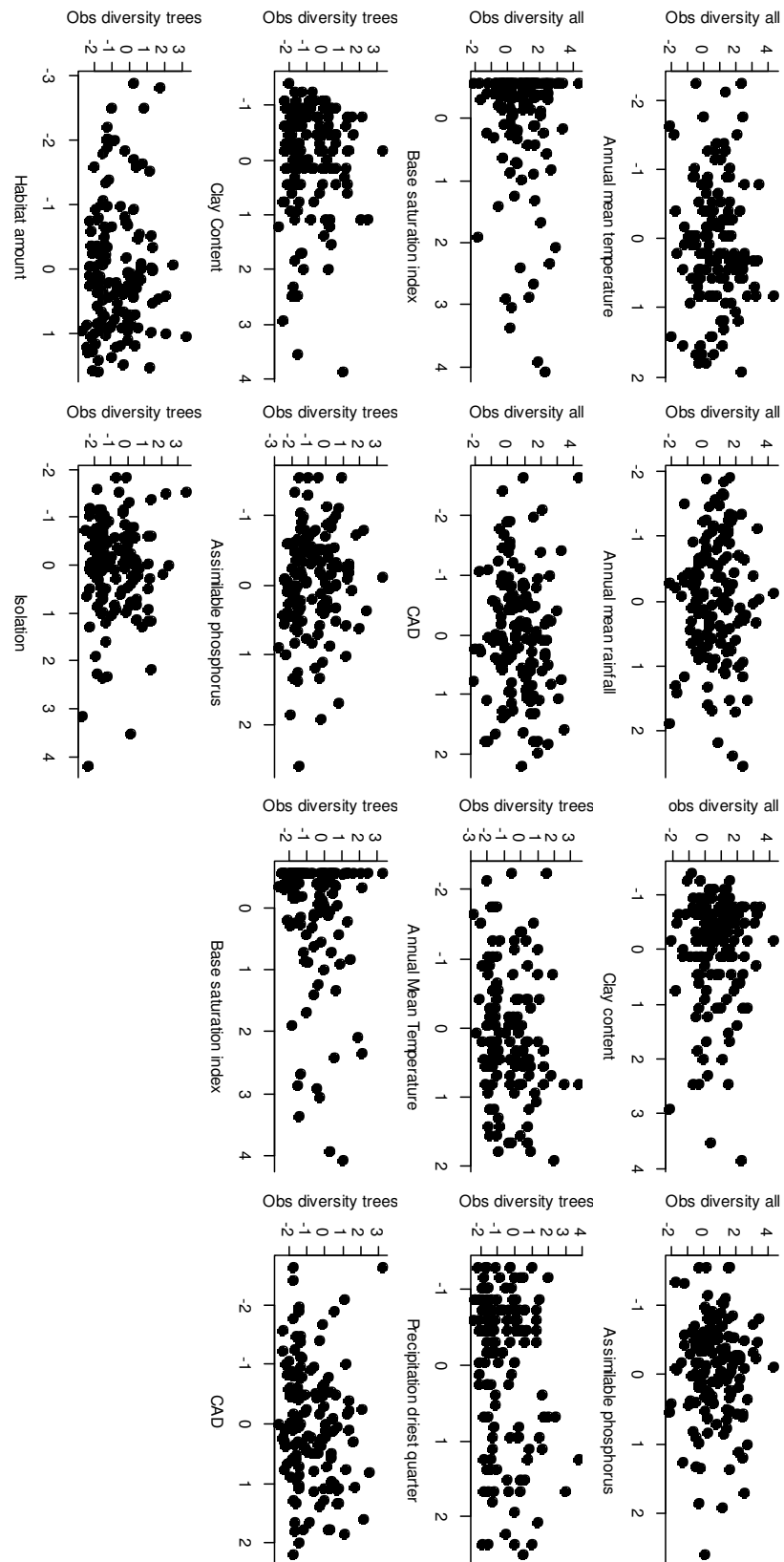


Supplementary Figure 08. Correlation between the observed diversity, dark diversity, completeness and species pool using Spearman rank correlations for herbs data.

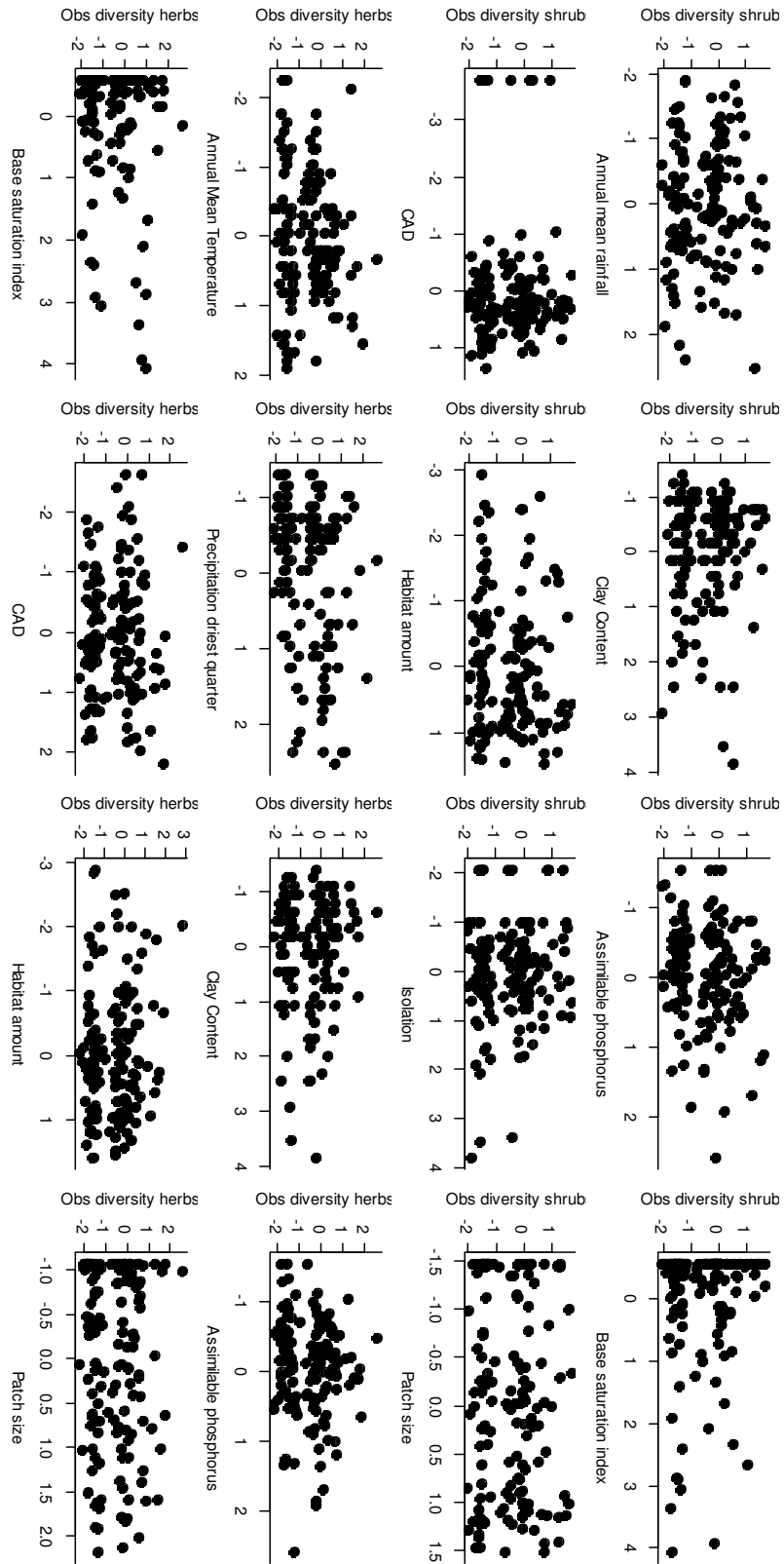


Supplementary Figure 09. Correlation between the observed diversity, dark diversity, completeness and species pool using Spearman rank correlations for vines data.

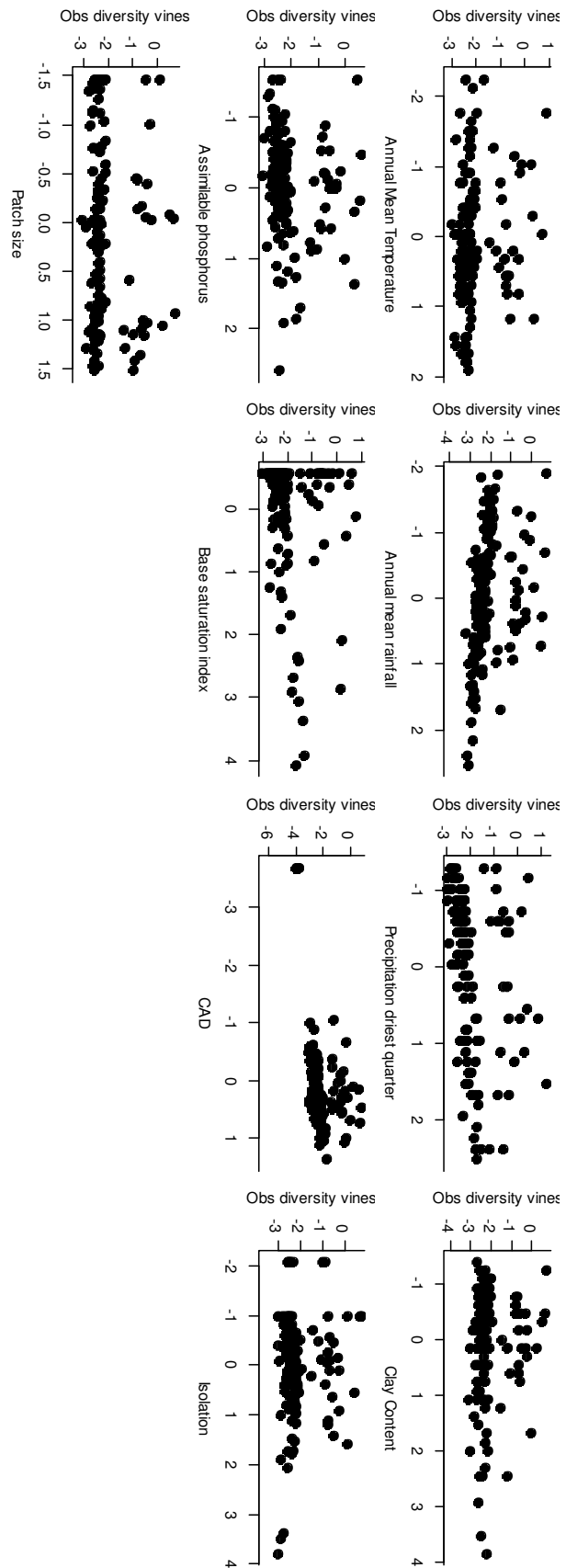
Supplementary Material 5



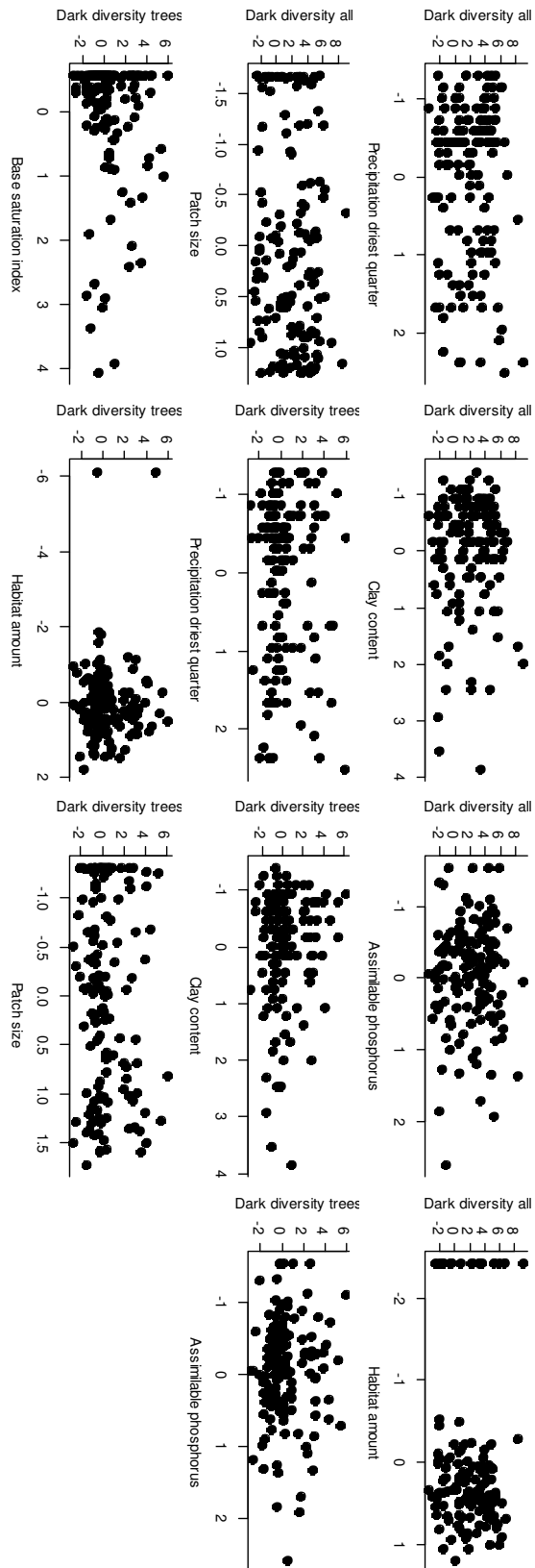
Supplementary Figure 10. Non-significant models for observed diversity of all plant lifeforms and trees.



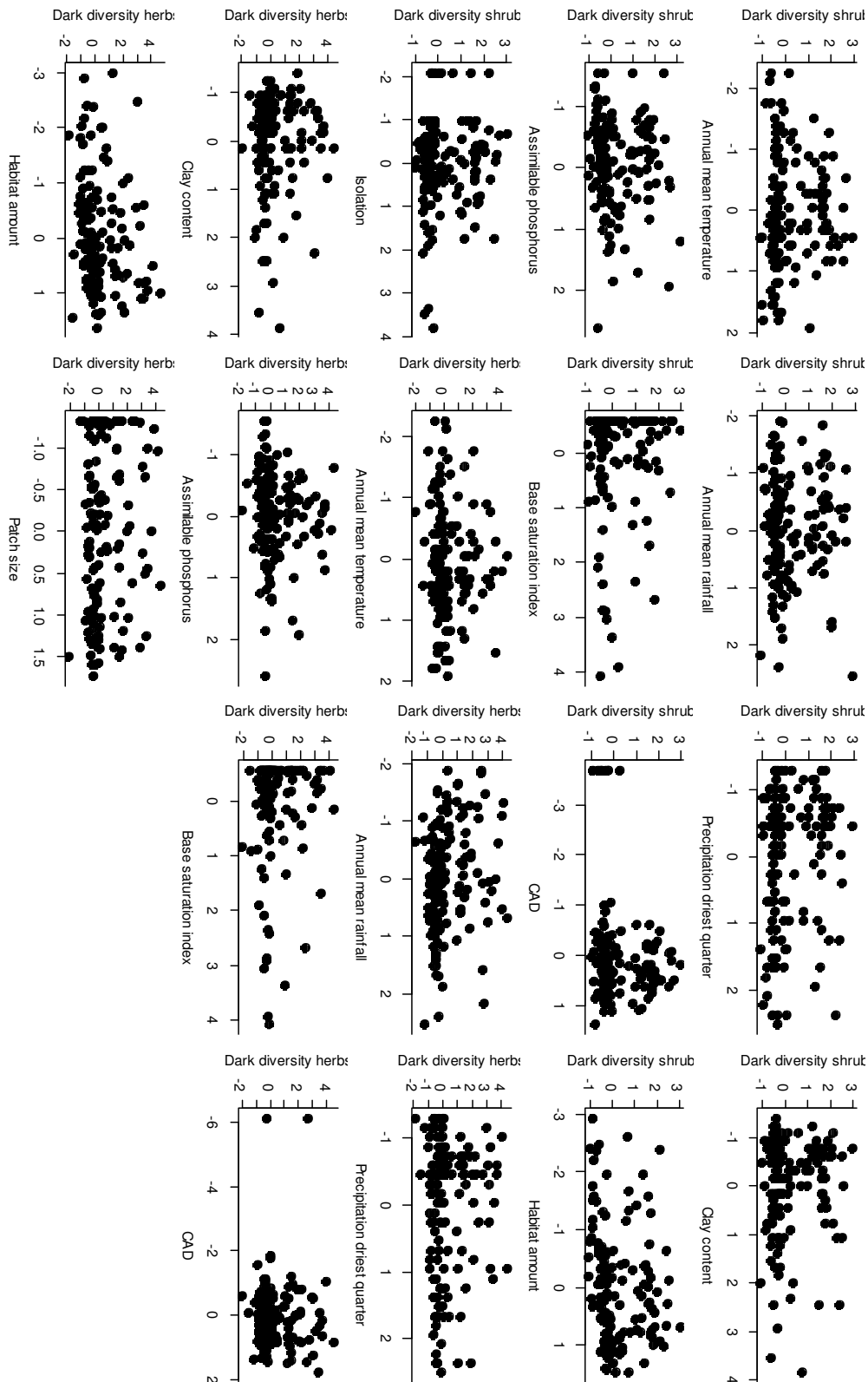
Supplementary Figure 11. Non-significant models for observed diversity of shrubs and herbs.



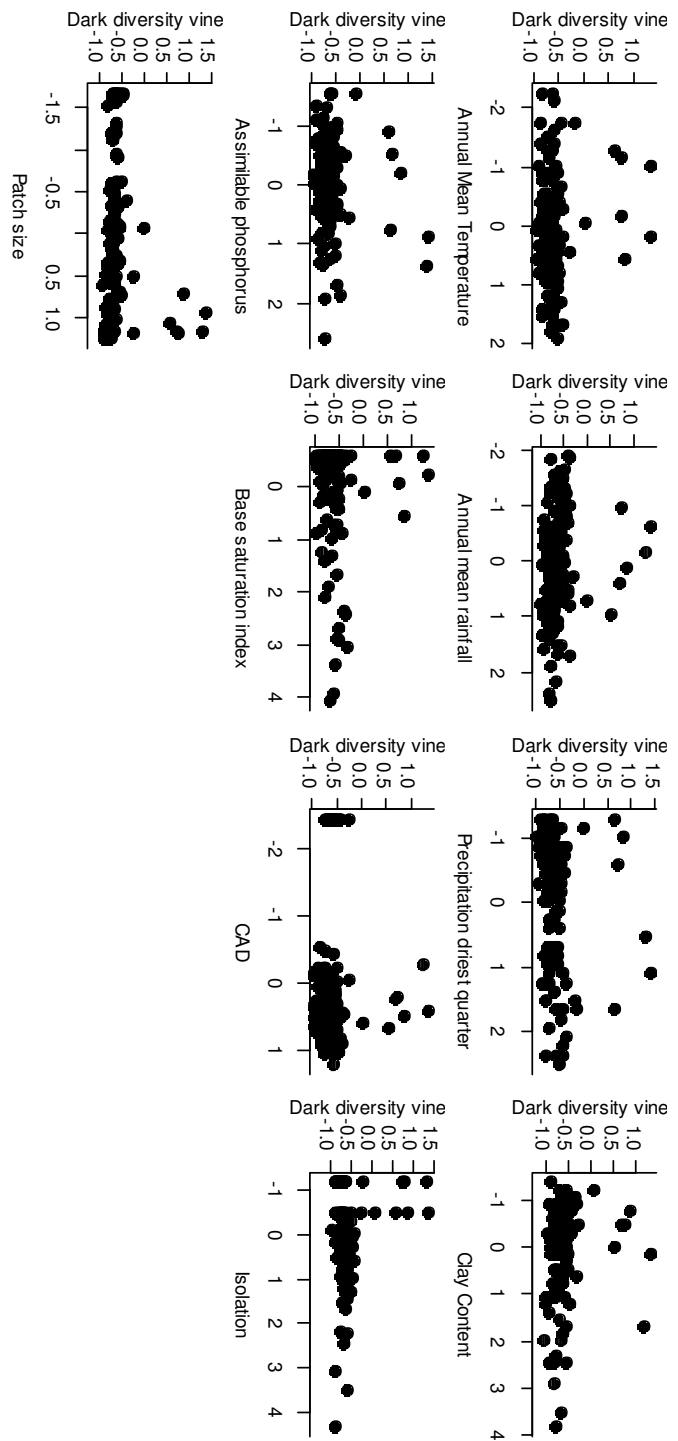
Supplementary Figure 12. Non-significant models for observed diversity of vines.



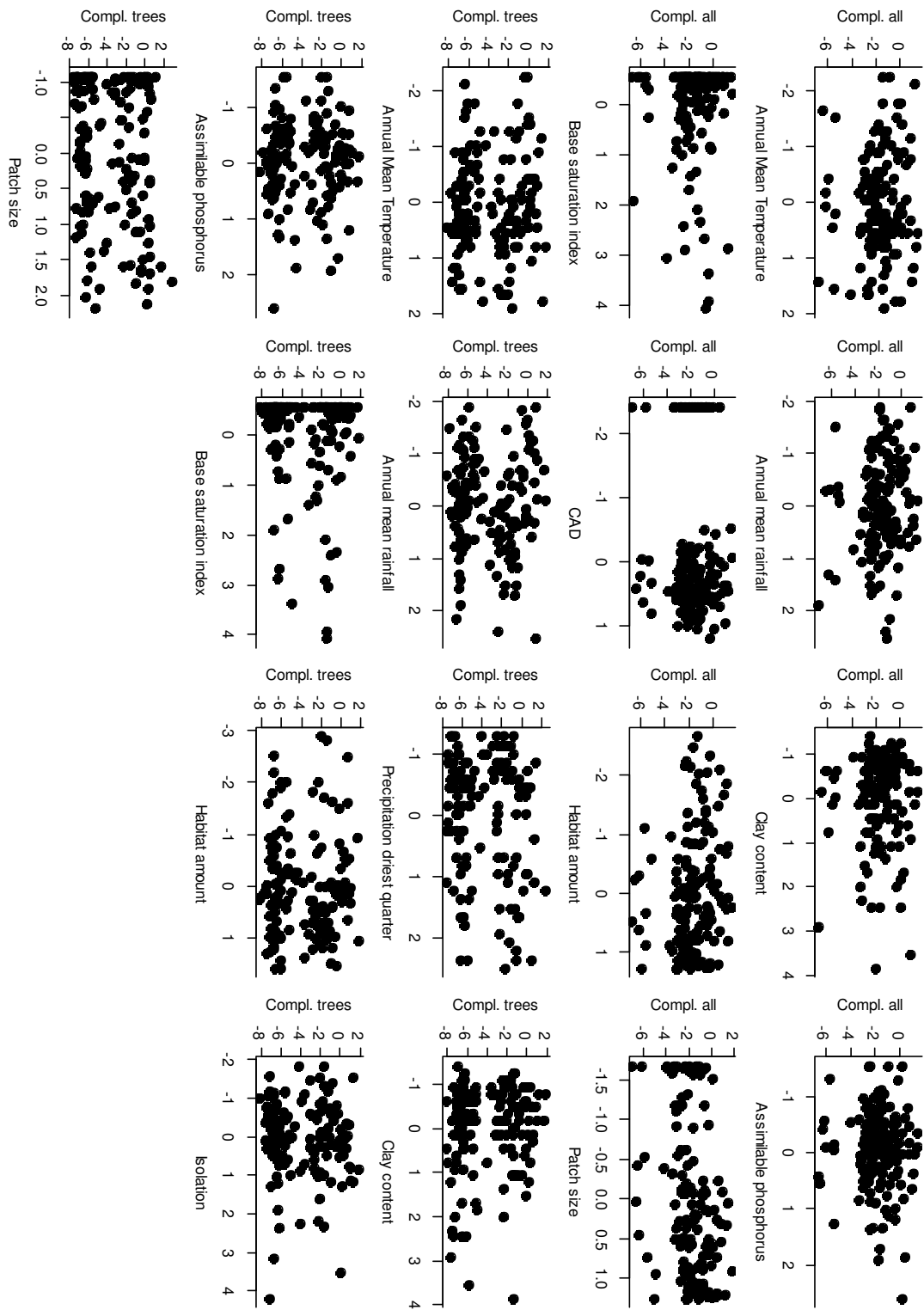
Supplementary Figure 13. Non-significant models for dark diversity of all plant lifeforms and trees.



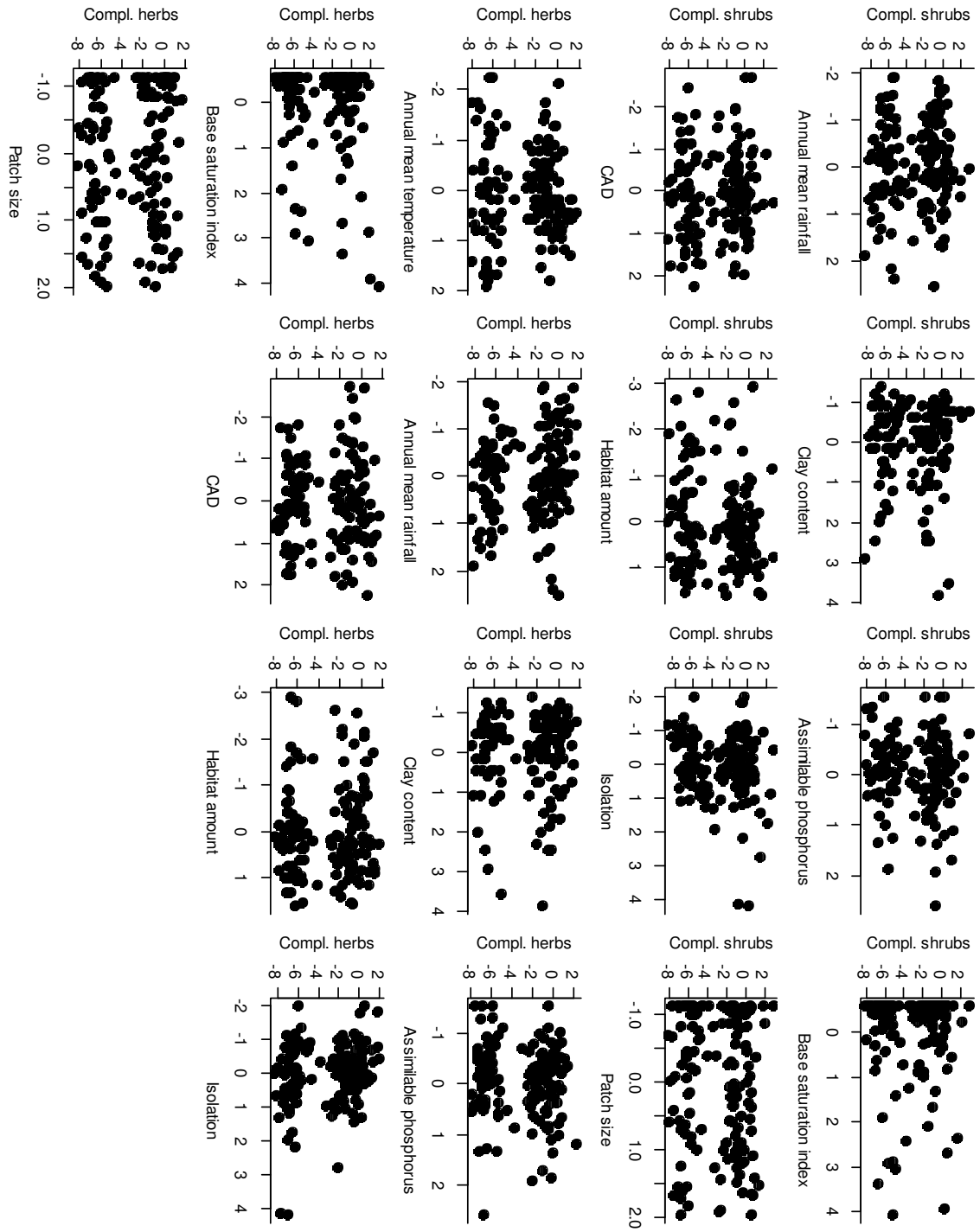
Supplementary Figure 14. Non-significant models for dark diversity of shrubs and herbs.



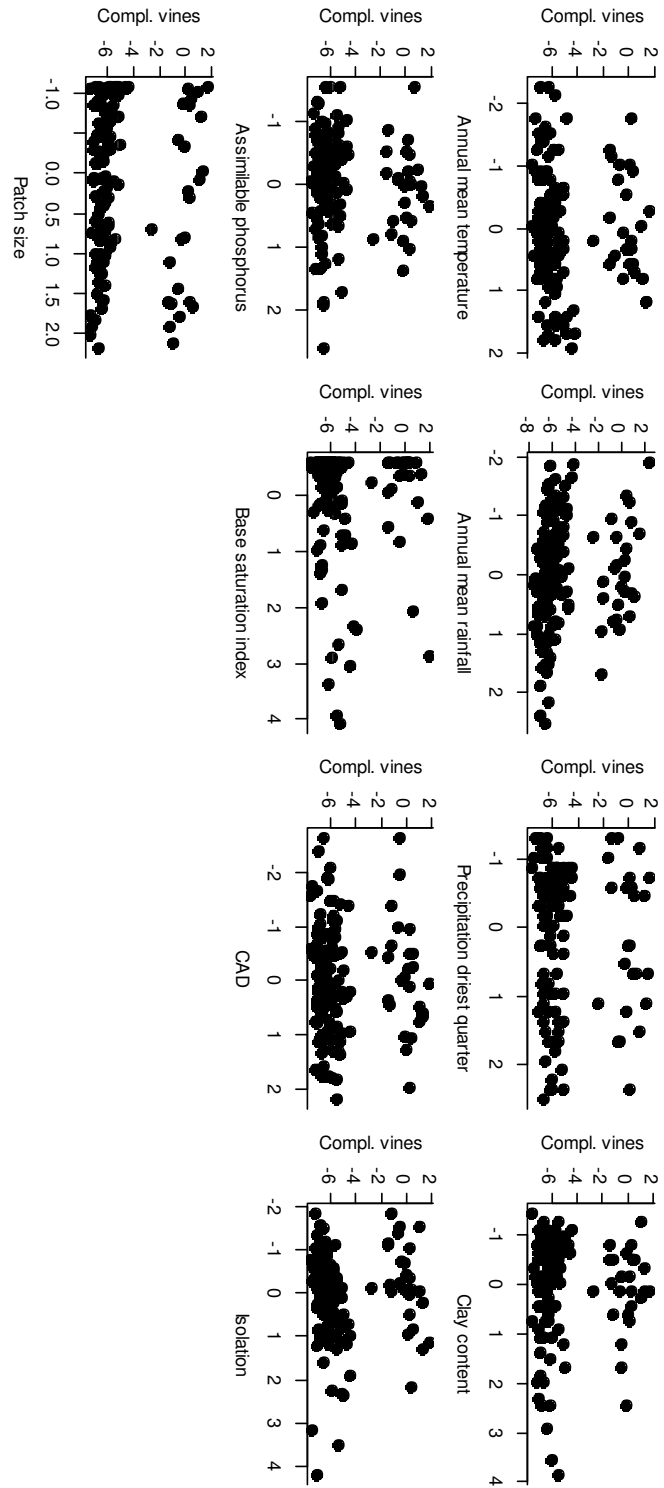
Supplementary Figure 15. Non-significant models for dark diversity of vines.



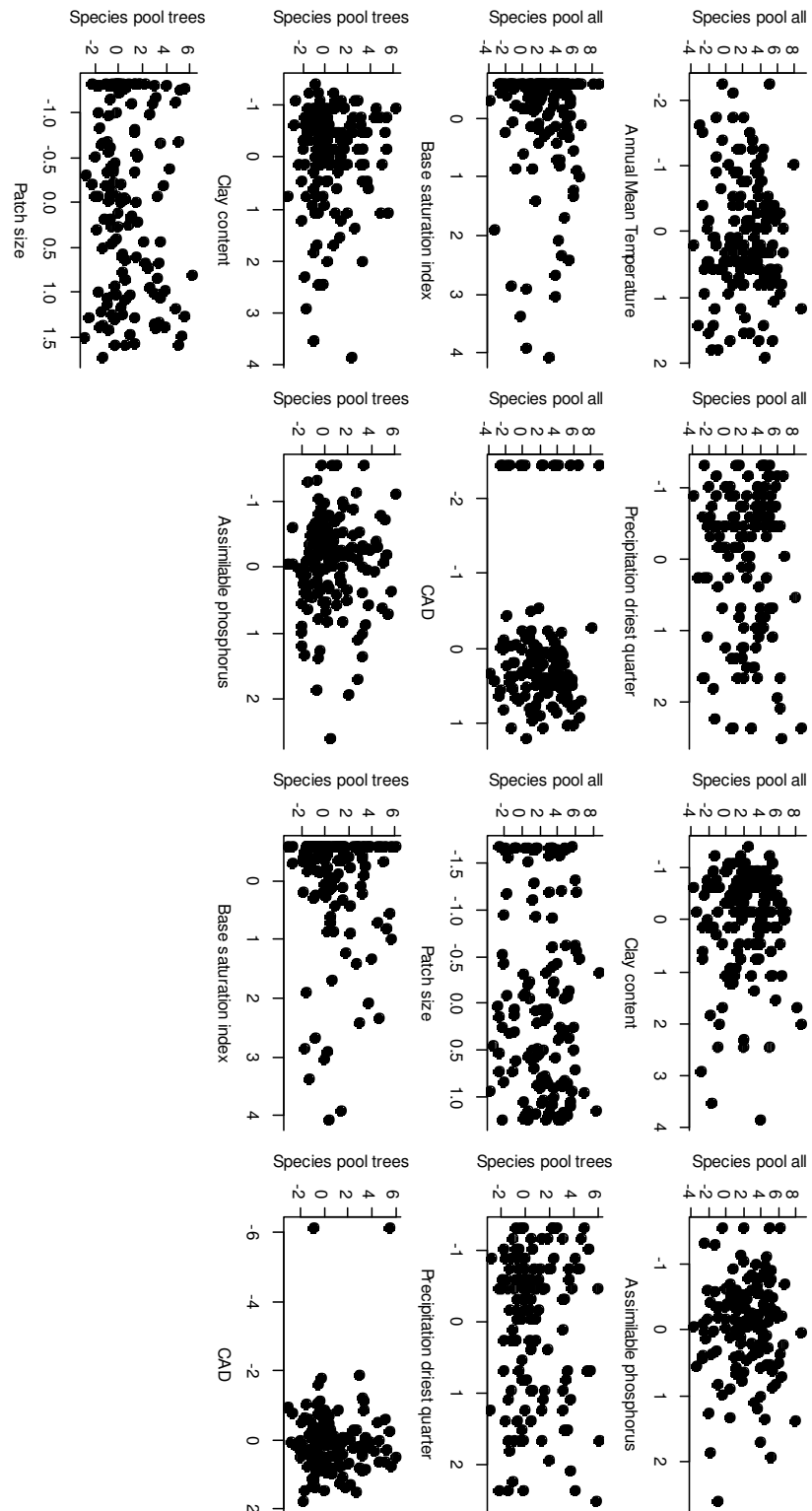
Supplementary Figure 16. Non-significant models for completeness of all plant lifeforms and trees.



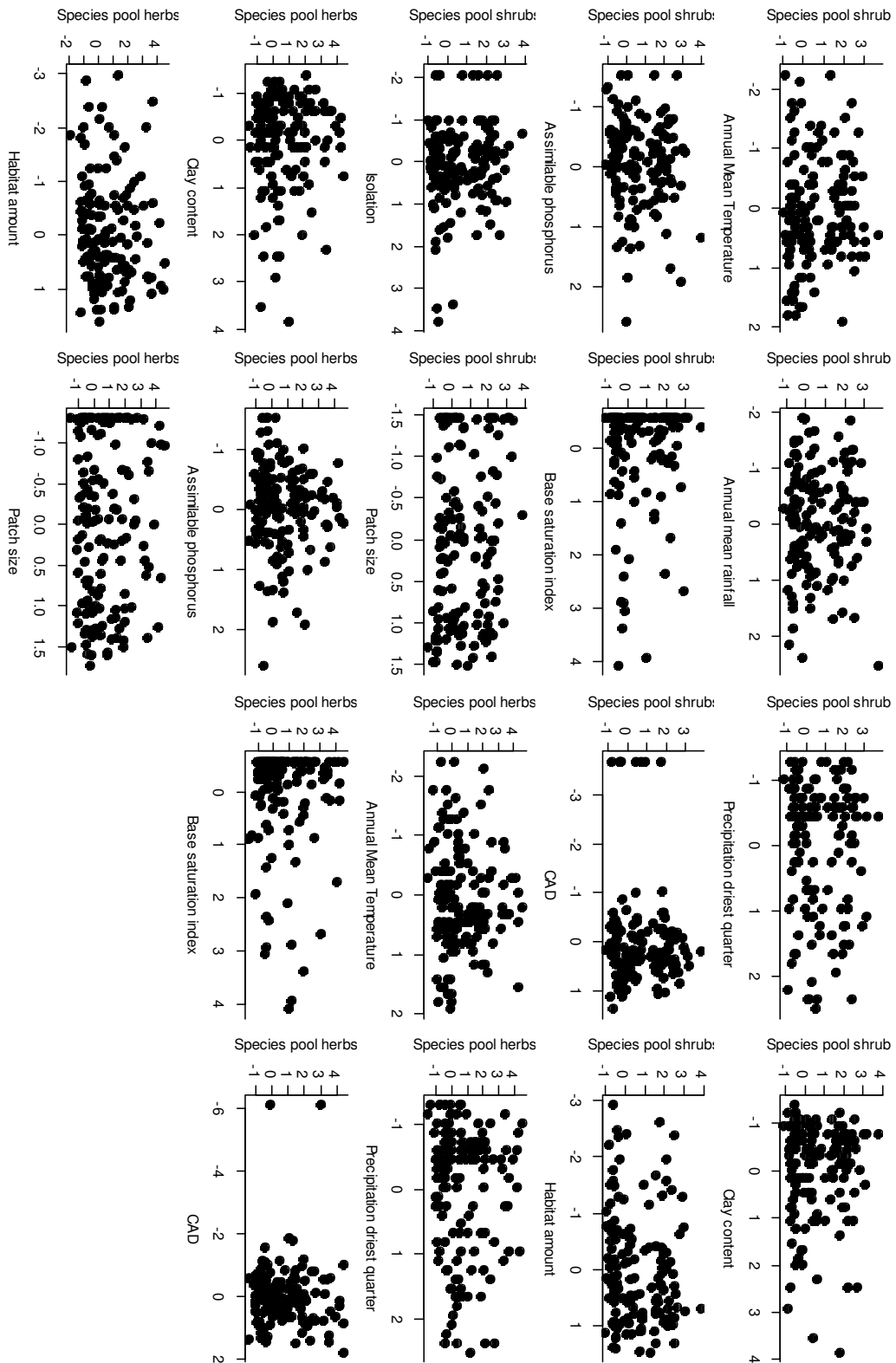
Supplementary Figure 17. Non-significant models for completeness of shrubs and herbs.



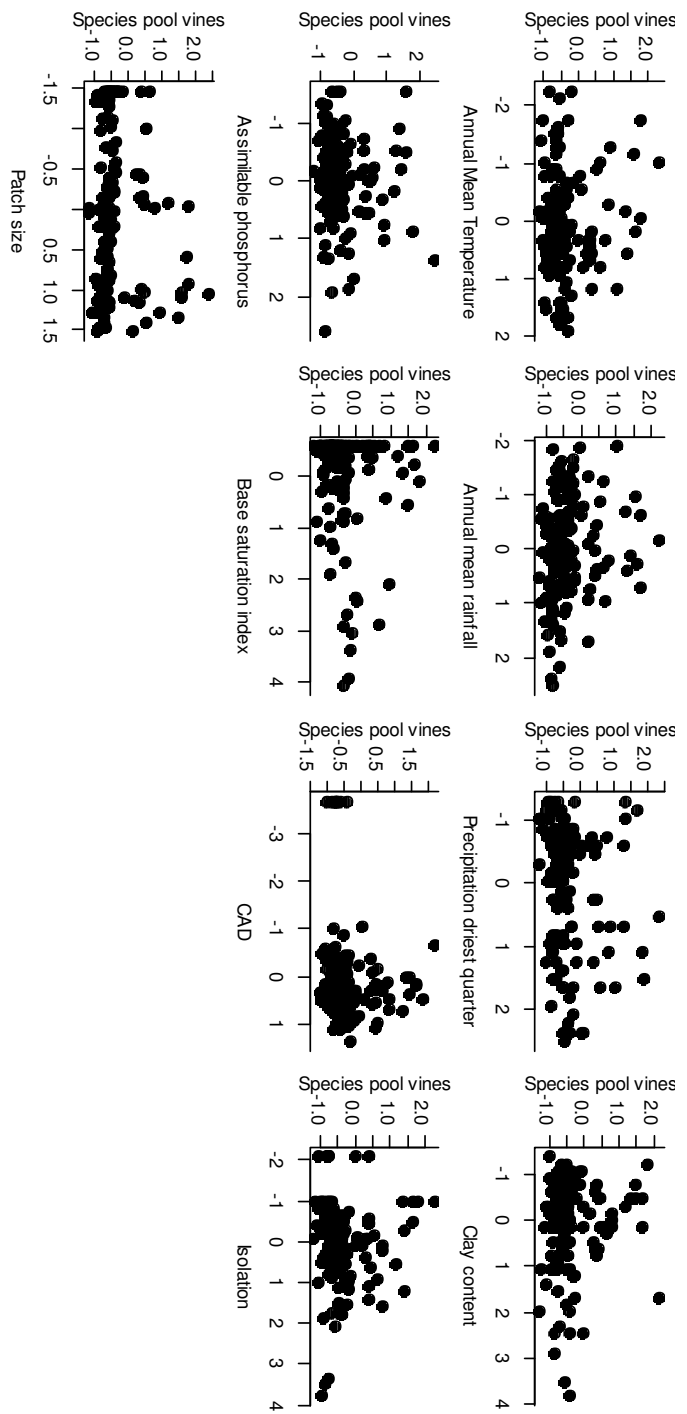
Supplementary Figure 18. Non-significant models for completeness of vines.



Supplementary Figure 19. Non-significant models for species pool of all plant lifeforms and trees.



Supplementary Figure 20. Non-significant models for species pool of shrubs and herbs.



Supplementary Figure 21. Non-significant models for species pool of vines.

14 CONCLUSÃO GERAL

Diante do cenário aqui apresentado, podemos traçar um quadro para entender como as perturbações antrópicas no ecossistema da Caatinga dependem da fertilidade do solo e de variáveis climáticas. Embora os distúrbios agudos sejam importantes para entender o destino de um ecossistema, avaliar o papel dos distúrbios crônicos é crucial para os biomas tradicionalmente conduzidos por humanos muito antes da chegada de quaisquer fronteiras agrícolas. Nossos resultados mostram que a perturbação humana é espacialmente previsível e não pode ser dissociada das variáveis ambientais: áreas com mais recursos para ocupação humana possivelmente levaram a um aumento na densidade de pessoas e animais dentro dos povoamentos de vegetação da Caatinga, apoiando uma conexão causal entre variáveis ambientais e a degradação da vegetação. Esses *drivers* irão moldar a forma como as pessoas usam os recursos naturais e, portanto, o destino da Caatinga. A diversidade escura é um conceito novo e útil para indicar quantas espécies estão escondidas atrás de suas espécies observadas em uma comunidade. Neste estudo, o clima, a quantidade e isolamento de fragmentos parecem ser os mais fortes preditores não apenas da riqueza vegetal, mas também da diversidade escura. Nossos resultados enfatizam fortemente que os esforços para conservar e restaurar a Caatinga utilizando diferentes métricas de diversidade pode contribuir para tomadas de decisão mais concisas e assertivas. Portanto, áreas com maior concentração de chuva e maior quantidade de habitat devem ser prioritárias para conservação, pois apresentam maior diversidade observada e menor número de espécies ausentes. Com a biodiversidade global diminuindo rapidamente, é vital entender os impulsionadores da biodiversidade para priorizar a conservação e tornar o gerenciamento mais eficiente para a vegetação da Caatinga.

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