



VINÍCIUS ANDRADE MAIA

**DINÂMICA DO CARBONO E SUAS RELAÇÕES COM
FUNCIONALIDADE E DIVERSIDADE EM FLORESTAS
TROPICAIS BRASILEIRAS EXTRA-AMAZÔNICAS**

LAVRAS – MG

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Tese apresentada à Universidade Federal de
Lavras, como parte das exigências do Programa
de Pós-Graduação em Engenharia Florestal,
área de concentração em Ecologia Florestal,
para a obtenção do título de Doutor.

Prof. Dr. Rubens Manoel Dos Santos
Orientador

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CARBON DYNAMICS AND ITS RELATIONSHIP WITH FUNCTIONALITY AND
DIVERSITY IN BRAZILIAN EXTRA-AMAZON TROPICAL FORESTS**

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RESUMO

As mudanças climáticas alteram de forma significativa o ciclo do carbono e afetam a capacidade das florestas tropicais de manter serviços ecossistêmicos essenciais. Esses ecossistemas, responsáveis por grande parte da biomassa terrestre, enfrentam pressões crescentes relacionadas à elevação da temperatura, variações de precipitação e aumento da mortalidade de árvores. Nesse cenário, traços funcionais e diversidade funcional das espécies assumem papel central, pois influenciam a produtividade, a resiliência e a estabilidade das florestas frente a distúrbios ambientais. O objetivo deste estudo é compreender como esses fatores modulam os estoques e a estocagem de carbono em florestas tropicais, visando ampliar o conhecimento sobre sua funcionalidade e subsidiar estratégias de conservação e manejo sustentável.

Palavras-chave: florestas tropicais; dinâmica do carbono; diversidade

ABSTRACT

Climate change significantly alters the carbon cycle and affects the ability of tropical forests to sustain essential ecosystem services. These ecosystems, which hold a substantial share of global biomass, face increasing pressures related to rising temperatures, changes in precipitation patterns, and higher tree mortality rates. In this context, functional traits and functional diversity play a central role, as they influence forest productivity, resilience, and stability under environmental disturbances. This study aims to understand how these factors shape carbon stocks and storage in tropical forests, thereby advancing knowledge on ecosystem functioning and supporting conservation and sustainable management strategies.

Keywords: tropical forests; carbon dynamics; functional diversity.

INDICADORES DE IMPACTO

O presente trabalho impacta diretamente os Objetivos de Desenvolvimento Sustentável (ODS): Ação Contra a Mudança Global do Clima e Vida Terrestre, ao contribuir para o avanço do conhecimento sobre os mecanismos ecológicos que regulam a dinâmica do carbono em florestas tropicais brasileiras extra-amazônicas. A pesquisa evidencia a importância da diversidade e dos traços funcionais das espécies na manutenção dos estoques e da estocagem de carbono, revelando que florestas mais diversas tendem a apresentar maior estabilidade e resiliência frente às mudanças climáticas. Os resultados obtidos possuem relevância científica e social, pois auxiliam na formulação de estratégias de manejo florestal sustentável, conservação da biodiversidade e mitigação das emissões de gases de efeito estufa. Do ponto de vista tecnológico, o estudo empregou ferramentas analíticas e modelagens avançadas para estimar o potencial de estocagem de carbono e identificar padrões funcionais que maximizam a produtividade ecológica, fornecendo subsídios aplicáveis a políticas públicas e a programas de restauração ecológica. Economicamente, o fortalecimento do conhecimento sobre o papel funcional das espécies pode orientar práticas de uso sustentável da terra e manejo florestal de baixo impacto, promovendo a valorização dos serviços ecossistêmicos e a captação de recursos via créditos de carbono e mecanismos de compensação ambiental. Culturalmente, a pesquisa reforça a importância das florestas como patrimônio natural e como base de identidades locais, incentivando práticas de conservação integradas aos modos de vida das comunidades que dependem desses ecossistemas. Em termos territoriais, os resultados são especialmente relevantes para regiões extra-amazônicas do Brasil, onde as florestas tropicais enfrentam crescente pressão antrópica e carecem de políticas de manejo adaptadas às suas particularidades ecológicas. Assim, o trabalho apresenta impactos potenciais de grande alcance, tanto na dimensão científica quanto na socioambiental, ao fortalecer o diálogo entre ciência, gestão ambiental e políticas de mitigação climática em consonância com a Agenda 2030 da ONU.

IMPACT INDICATORS

The present study directly contributes to the Sustainable Development Goals (SDGs) Climate Action and Life on Land by advancing knowledge on the ecological mechanisms regulating carbon dynamics in extra-Amazonian Brazilian tropical forests. The research highlights the importance of species diversity and functional traits in maintaining carbon stocks and storage, revealing that more diverse forests tend to exhibit greater stability and resilience in the face of climate change. The findings hold both scientific and social relevance, as they support the development of strategies for sustainable forest management, biodiversity conservation, and the mitigation of greenhouse gas emissions. From a technological standpoint, the study employed advanced analytical tools and modeling approaches to estimate carbon storage potential and identify functional patterns that maximize ecological productivity, providing insights applicable to public policies and ecological restoration programs. Economically, strengthening knowledge about the functional role of species can guide sustainable land-use practices and low-impact forest management, promoting the valuation of ecosystem services and the generation of resources through carbon credits and environmental compensation mechanisms. Culturally, the research reinforces the importance of forests as natural heritage and as a foundation of local identities, encouraging conservation practices that are integrated with the livelihoods of communities that depend on these ecosystems. From a territorial perspective, the results are particularly relevant to Brazil's extra-Amazonian regions, where tropical forests face increasing anthropogenic pressure and lack management policies tailored to their specific ecological characteristics. Thus, this work presents potential impacts of broad scope—both scientifically and socio-environmentally—by strengthening the dialogue between science, environmental management, and climate mitigation policies, in alignment with the United Nations 2030 Agenda.

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PRIMEIRA PARTE

1 INTRODUÇÃO

O carbono desempenha papel central no funcionamento do sistema terrestre e na manutenção da vida, integrando processos biogeoquímicos essenciais, como fotossíntese, respiração e decomposição, que regulam a produtividade primária e influenciam o clima (Archer, 2010; Friedlingstein *et al.*, 2025; Li *et al.*, 2018). Desde a Revolução Industrial, entretanto, a intensificação do uso de combustíveis fósseis e as mudanças no uso da terra alteraram profundamente o ciclo do carbono, resultando no aumento expressivo das concentrações atmosféricas de CO₂ e no consequente fortalecimento do efeito estufa (Keenan *et al.*, 2015; Le Quéré *et al.*, 2018; Friedlingstein *et al.*, 2025). Esse processo intensifica o aquecimento global, promovendo impactos ambientais e sociais de grande escala, com destaque para a alteração nos regimes de seca e a perda de estabilidade dos ecossistemas (Pachauri; Meyer, 2014; Mcdowell *et al.*, 2018).

Nesse contexto, as florestas exercem papel estratégico, uma vez que concentram a maior parte da biomassa terrestre e atuam como importantes sumidouros de carbono (Mitchard, 2018; Pan *et al.*, 2011, 2013). Estima-se que aproximadamente 75% da produtividade primária bruta terrestre e 80% da biomassa estejam associadas à cobertura florestal, com destaque para as florestas tropicais, que apresentam os maiores estoques de carbono e a maior produtividade anual (Mitchard, 2018; Pan *et al.*, 2011). Entretanto, mudanças climáticas, desmatamento e outros distúrbios podem comprometer essa função, colocando em risco a estabilidade dos estoques e a capacidade de sequestro de carbono das florestas tropicais (Hubau *et al.*, 2020; Maia *et al.*, 2020; Bennet *et al.*, 2023).

Além dos fatores ambientais, os traços funcionais e a diversidade funcional das espécies influenciam diretamente a dinâmica do carbono florestal (Aguirre-Gutiérrez *et al.*, 2022; Bialic-Murphy *et al.*, 2024). Florestas mais diversas, compostas por espécies com traços funcionais contrastantes, tendem a apresentar maior produtividade e maior estabilidade temporal, resultado de mecanismos como complementaridade de nicho, assincronia entre espécies e interações facilitadoras (Jucker *et al.*, 2014; Tobner *et al.*, 2016; Reich, 2014). Nesse sentido, compreender a interação entre fatores ambientais e diversidade funcional é essencial para avaliar a resiliência das florestas tropicais frente às mudanças globais e para subsidiar estratégias de manejo e conservação voltadas à manutenção dos estoques de carbono.

2 REFERENCIAL TEÓRICO

2.1 Carbono, planeta e seres vivos

O carbono constitui um dos elementos fundamentais para o funcionamento do sistema terrestre e para a manutenção da vida, pois participa de maneira direta e indireta de diversos processos biogeoquímicos e está intrinsicamente associado ao metabolismo dos organismos vivos. O ciclo do carbono envolve a troca contínua desse elemento entre a atmosfera, a biosfera, os solos e os oceanos, abrangendo fluxos que podem se dar em escalas de tempo que variam de décadas até milhares de anos (Archer, 2010; Friedlingstein *et al.*, 2025). Entre os processos essenciais desse ciclo está a fotossíntese, que representa a principal via de entrada da energia solar no sistema terrestre (Li *et al.*, 2018). A partir dela, a energia se propaga pela cadeia trófica, da produtividade primária aos níveis mais elevados, configurando-se como processo essencial para a dinâmica ecológica (Archer, 2010; Li *et al.*, 2018). O fluxo de carbono ocorre por meio de mecanismos como fotossíntese, respiração, decomposição e mineralização, que, em conjunto, integram-se a outros ciclos biogeoquímicos essenciais, como os do oxigênio, do nitrogênio e da água. A interação entre esses ciclos regula a produtividade primária, influencia o clima, condiciona a disponibilidade de água e sustenta diversos serviços ecossistêmicos (Friedlingstein *et al.*, 2025; Mitchard, 2018).

A dinâmica do sistema terrestre, e em especial o ciclo do carbono, passou a ser fortemente impactada desde a Revolução Industrial, quando a queima de combustíveis fósseis se intensificou. Além dessa fonte, as mudanças no uso da terra e o desmatamento também exerceram papel relevante, alterando de forma profunda os fluxos de carbono (Keenan *et al.*, 2015; Keenan; Williams, 2018; Le Quéré *et al.*, 2018; Mitchard, 2018). Como resultado, a concentração atmosférica de CO₂ aumentou de 277 ppm em 1750 para 422.45 ppm em 2024, sendo inicialmente impulsionada pelas mudanças no uso da terra até meados do século XX e, posteriormente, pela crescente queima de combustíveis fósseis (Dlugokencky; Tans, 2025; Friedlingstein *et al.*, 2025; Le Quéré *et al.*, 2018).

O dióxido de carbono presente na atmosfera atua interceptando a radiação refletida pela superfície terrestre, retendo parte do calor e permitindo que outra parte seja liberada para o espaço. Esse mecanismo, conhecido como efeito estufa, constitui um processo natural indispensável para a regulação do clima e para a manutenção da vida no planeta, configurando-se como um serviço ecossistêmico de escala global. Contudo, o aumento das emissões e das concentrações atmosféricas de CO₂ intensifica o efeito estufa, resultando em maior retenção de calor e elevação da temperatura média global (Keenan; Williams, 2018; Pachauri; Meyer, 2014). O aquecimento global, por sua vez, gera impactos abrangentes sobre os organismos vivos, modificando suas interações ecológicas e suas relações com o ambiente (McDowell *et al.*, 2018). Além disso, as mudanças climáticas estão associadas a alterações nos regimes de

seca, com variações na intensidade, frequência e duração desses eventos (Pachauri; Meyer, 2014). Tais transformações afetam profundamente a dinâmica do sistema terrestre, em especial a biosfera, e repercutem sobre atividades produtivas, industriais e agrícolas, trazendo consequências diretas para a economia, a sociedade e a qualidade de vida humana (Friedlingstein *et al.*, 2025).

A intensidade das atividades humanas e seus impactos sobre o ambiente atingiram tal magnitude que diversos autores passaram a caracterizar o período atual como uma nova época geológica, o Antropoceno (Christenhusz; Govaerts, 2025; Roberts; Boivin; Kaplan, 2018). Esse conceito está relacionado à abrangência das ações antrópicas, cuja escala e intensidade produzem padrões ambientais inéditos, que não ocorreriam de forma natural sem a intervenção humana (Roberts; Boivin; Kaplan, 2018). No âmbito terrestre, as florestas se destacam pelo papel central como principais sumidouros de carbono (Mitchard, 2018; Pan *et al.*, 2013). O sequestro de carbono realizado pela fotossíntese representa um serviço ecossistêmico essencial, pois sustenta a produtividade primária, fornece energia para a cadeia trófica e contribui para a regulação do clima global. Contudo, fatores como desmatamento, queimadas, mudanças climáticas e outros distúrbios colocam em risco essa função, podendo levar as florestas a deixarem de atuar como sumidouros e a se tornarem fontes líquidas de carbono nas próximas décadas (Hubau *et al.*, 2020; Maia *et al.*, 2020).

Em escala global, estima-se que aproximadamente 75% da produtividade primária bruta terrestre e 80% da biomassa estejam concentradas na cobertura florestal, com destaque para as florestas tropicais, que apresentam os maiores estoques de carbono e a maior produtividade anual (Mitchard, 2018; Pan *et al.*, 2011, 2013). Contudo, tais valores podem ser significativamente alterados nas próximas décadas em função das mudanças climáticas, que afetam diretamente a vegetação, especialmente por meio da intensificação de eventos de seca e das variações de temperatura (Bennet *et al.*, 2023). Essas transformações repercutem não apenas sobre o ciclo do carbono, mas também sobre a ciclagem de nutrientes e o ciclo hidrológico, provocando modificações no regime de chuvas e consequências relevantes para a agricultura e a segurança alimentar. Como as florestas tanto influenciam quanto são impactadas pelo clima, esse processo pode desencadear um efeito cascata, no qual a perda florestal associada ao desmatamento se torna um agravante.

2.2 Dinâmica do carbono em florestas tropicais

Embora a radiação solar seja o principal fator que sustenta a atividade biológica das plantas, outros elementos exercem papel igualmente relevante nos processos fotossintéticos. Entre eles, destacam-se a concentração de dióxido de carbono na atmosfera, a disponibilidade

de água, a temperatura e a oferta de nutrientes no solo (Boisvenue; Running, 2006). Assim, atributos relacionados às condições climáticas e edáficas, bem como às suas interações, são fundamentais para compreender os mecanismos que regulam a produtividade vegetal. As respostas fisiológicas das plantas às condições ambientais estão fortemente associadas aos filtros ambientais que se manifestam em diferentes escalas espaciais e temporais (Malhi, 2012; McDowell *et al.*, 2018).

O aumento da temperatura pode elevar o déficit de pressão de vapor no ar, intensificando as taxas de transpiração e impactando negativamente a produtividade vegetal devido à maior perda de água (Boisvenue; Running, 2006; Corlett, 2016; Malhi, 2012). O metabolismo das plantas é fortemente influenciado pela temperatura, que determina a capacidade fotossintética e, conseqüentemente, a produtividade; a faixa ótima para a produtividade situa-se entre 15 e 25 °C (Boisvenue; Running, 2006; Hopkins; Hüner, 2004). Evidências recentes indicam, entretanto, que os estoques de carbono em florestas tropicais úmidas podem apresentar resiliência desde que a temperatura máxima não ultrapasse 32,2 °C (Sullivan *et al.*, 2020).

A água desempenha papel essencial, sendo o principal componente celular e um solvente universal, permitindo a ocorrência de reações químicas vitais para o metabolismo. Devido à sua importância na fotossíntese, a produtividade vegetal geralmente apresenta relação positiva com a precipitação anual; contudo, acima de determinado limiar (aproximadamente 3.000 mm/ano), essa relação pode se inverter (Boisvenue; running, 2006; Schuur, 2003; Taylor *et al.*, 2017). Esse efeito negativo é atribuído à lixiviação de nutrientes, redução da disponibilidade de oxigênio no solo e à diminuição da radiação incidente devido à elevada nebulosidade (Schuur, 2003). A interação entre temperatura média anual e precipitação constitui um importante preditor da produtividade primária e da ciclagem de carbono (Taylor *et al.*, 2017). Em regiões de menores temperaturas médias anuais (até 20 °C), a precipitação pode ter efeito adverso, especialmente em áreas de maior altitude, onde a saturação do solo pode levar a condições de anoxia (Taylor *et al.*, 2017).

O aumento da concentração de CO₂ na atmosfera pode teoricamente favorecer a produtividade primária, uma vez que maior quantidade do gás estaria disponível para a fotossíntese (Huntingford *et al.*, 2013; Lewis *et al.*, 2009). Esse fenômeno, denominado fertilização da atmosfera, tem sido foco de diversos estudos nas últimas décadas. Nesse contexto, os efeitos positivos da elevação do CO₂ sobre a fotossíntese poderiam superar os impactos negativos do aumento da temperatura sobre a respiração vegetal. As principais questões relacionadas à fertilização atmosférica referem-se às respostas fisiológicas das plantas

e à resiliência dos ecossistemas e florestas frente ao incremento das concentrações de CO₂ (Hofhansl *et al.*, 2016; Lewis *et al.*, 2009).

Análises de diferentes modelos biogeoclimáticos indicam que, até o final do século XXI, apenas as florestas tropicais da América apresentariam perda de biomassa, enquanto as florestas asiáticas e africanas demonstrariam maior resiliência. Contudo, incertezas persistem devido às respostas fisiológicas distintas entre espécies e tipos de floresta (Corlett, 2016; McDowell *et al.*, 2018). O aumento do CO₂ também pode melhorar a eficiência no uso da água durante a fotossíntese, embora haja evidências de que essa maior concentração possa, em algumas situações, afetar negativamente a produtividade (McDowell *et al.*, 2018). Além disso, o incremento nas taxas de crescimento decorrente do maior CO₂ disponível pode acelerar a dinâmica sucessional e favorecer a proliferação de lianas, aumentando a competição por recursos, reduzindo o crescimento e elevando a mortalidade de árvores (McDowell *et al.*, 2018). Outros fatores podem influenciar essas respostas, como aclimação a níveis mais elevados de CO₂, maior exposição a ventos e implicações fisiológicas associadas ao aumento do tamanho e altura das árvores (McDowell *et al.*, 2018). Por fim, efeitos interativos entre a concentração de CO₂ e a disponibilidade de nutrientes, especialmente nitrogênio, também podem modular a resposta das plantas, sendo que a limitação de nitrogênio tende a reduzir o efeito positivo da fertilização atmosférica (Norby *et al.*, 2010).

Os nutrientes desempenham papel central na produtividade e nos estoques de carbono das florestas (Cunha *et al.*, 2022; Norby *et al.*, 2010; Turner; Brenes-Arguedas; Condit, 2018). O fósforo, por exemplo, é essencial para o metabolismo vegetal, uma vez que faz parte do nucleotídeo ATP, responsável pelo armazenamento de energia em ligações químicas. A limitação de fósforo tem sido amplamente discutida, considerando que algumas espécies desenvolveram estratégias adaptativas para lidar com sua baixa disponibilidade (Cunha *et al.*, 2022; Turner; Brenes-Arguedas; Condit, 2018). Embora certas espécies sejam sensíveis à escassez desse nutriente, a comunidade florestal como um todo tende a ser resiliente, devido à presença de espécies tolerantes (Turner; Brenes-Arguedas; Condit, 2018). Esse fenômeno dá origem a um paradigma acerca dos efeitos da limitação de fósforo sobre a produtividade vegetal, particularmente em função de interações com outros nutrientes, como o nitrogênio (Dalling *et al.*, 2016). Os impactos da limitação de fósforo podem variar conforme a idade e os grupos funcionais das plantas, sendo mais pronunciados em indivíduos jovens (Alvarez-Clare; Mack; Brooks, 2013). No entanto, uma meta-análise realizada por Cleveland *et al.* (2011) demonstrou que o fósforo apresenta efeito positivo e significativo sobre a produtividade.

Entre os componentes que influenciam os estoques e a estocagem de carbono, a mortalidade de árvores se destaca, podendo ter papel mais determinante que o crescimento na predição de estoques de carbono e produtividade em florestas tropicais (Corlett, 2016; Johnson *et al.*, 2016; Maia *et al.*, 2020; McDowell *et al.*, 2018). Alterações nas condições ambientais e na disponibilidade de recursos têm contribuído para o aumento da mortalidade arbórea, impactando negativamente a produtividade primária e os estoques de carbono, especialmente na Bacia Amazônica, onde essa mortalidade vem crescendo nas últimas décadas (McDowell *et al.*, 2018). Diversos fatores ambientais podem atuar isoladamente ou de forma interativa sobre a mortalidade das árvores, incluindo aumentos de temperatura e do déficit de pressão de vapor, que afetam globalmente o metabolismo vegetal (Anderegg *et al.*, 2016; McDowell *et al.*, 2018). A prolongação dos períodos de seca também contribui para a mortalidade, principalmente por meio de falhas hidráulicas e alterações nas taxas de respiração, com árvores de maior porte sendo mais vulneráveis, resultando em perdas significativas de carbono (Corlett, 2016; Bennet *et al.*, 2023; McDowell *et al.*, 2018).

Embora o aumento do CO₂ atmosférico possa acelerar o crescimento, ele também pode elevar indiretamente a mortalidade, ao intensificar a dinâmica sucessional e a competição por recursos (McDowell *et al.*, 2018). O crescimento acelerado decorrente de maiores concentrações de CO₂ pode expor árvores a riscos fisiológicos relacionados ao tamanho e à altura, além de maior vulnerabilidade a ventos e eventos extremos (McDowell *et al.*, 2018). Fatores adicionais, como a competição com lianas — cuja abundância pode aumentar devido à seca e ao CO₂ elevado —, fogo e vento, também são preditores importantes da mortalidade arbórea (McDowell *et al.*, 2018).

Os mesmos fatores que determinam a mortalidade influenciam o crescimento vegetal, de forma que algumas árvores podem sobreviver, porém com crescimento reduzido devido à competição e escassez de recursos. A complexidade das interações entre esses fatores torna difícil avaliar a importância relativa de cada um e prever padrões de mortalidade em um mundo em transformação. Em síntese, é provável que as mudanças climáticas afetem negativamente os estoques de carbono e a produtividade das florestas tropicais, principalmente por meio das respostas fisiológicas de indivíduos, populações e comunidades (Anderegg *et al.*, 2016; Bennet *et al.*, 2023; Feng *et al.*, 2018; Maia *et al.*, 2020).

Além dos fatores ambientais, os traços funcionais e a diversidade funcional das espécies desempenham um papel importante na dinâmica do carbono florestal (Aguirre-Gutiérrez *et al.*, 2022; Bialic-Murphy *et al.*, 2024). Florestas diversas, particularmente aquelas compostas por espécies com traços funcionais distintos entre si, tendem a apresentar maior produtividade e

maior estabilidade temporal em comparação com comunidades menos diversas, um padrão relacionado a múltiplos mecanismos, incluindo complementaridade de nicho, assincronia entre espécies (complementariedade de nicho temporal) e interações facilitadoras (Bialic-Murphy *et al.*, 2024; Jucker *et al.*, 2014). A complementaridade de nicho permite que as espécies explorem os recursos de forma mais eficiente, com árvores ocupando diferentes estratos do dossel e profundidades radiculares, por exemplo, aumentando assim a produtividade em nível de comunidade e reduzindo a mortalidade por competição por recursos (Tilman, 1999; Díaz *et al.*, 2011). As características funcionais, particularmente a prevalência de estratégias aquisitivas caracterizadas por alta área foliar específica, baixa densidade da madeira e rápido crescimento, pode aumentar a produtividade e a eficiência no uso de recursos, enquanto traços funcionais conservativos predominam sob condições de estresse ou de limitação de recursos, promovendo a sobrevivência e a facilitação interespecífica (Reich, 2014). Além disso, a dispersão de traços funcionais (FDis) entre espécies coocorrentes está associada ao aumento da diferenciação de nicho, o que amplifica os efeitos da diversidade sobre a produtividade, mesmo em níveis constantes de riqueza de espécies (Bialic-Murphy *et al.*, 2024; Tobner *et al.*, 2016). Consequentemente, integrar os traços funcionais das espécies e a diversidade nas estratégias de manejo e conservação florestal é fundamental. Para avançar na compreensão desses processos e realizar predições mais confiáveis para cenários futuros, torna-se essencial a coleta de dados robustos em campo, fornecendo informações detalhadas para subsidiar a tomada de decisão em nível público.

3. CONSIDERAÇÕES FINAIS

As florestas tropicais são componentes centrais do sistema terrestre, desempenhando papel crucial no ciclo do carbono e na regulação climática. A análise da relação entre a dinâmica do carbono e traços funcionais e a diversidade funcional das comunidades revela-se essencial para compreender os mecanismos que sustentam a produtividade, a resiliência e a estabilidade desses ecossistemas diante das mudanças ambientais. Entretanto, sua relevância não se limita à funcionalidade, pois esses ambientes também representam importantes reservatórios de biodiversidade e reguladores de processos ecológicos em larga escala. Avançar no conhecimento sobre como a diversidade e a funcionalidade modulam estoques e fluxos de carbono é, portanto, indispensável para embasar estratégias de conservação e manejo sustentável que assegurem a persistência das florestas tropicais em um contexto de rápidas transformações globais.

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SEGUNDA PARTE

Artigo 1 - Temporal trends of carbon stock, sink, and tree species diversity in subtropical and subtropical Brazilian forests

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Abstract

Recent evidence indicates that Brazilian forests are shifting from persistent carbon sinks to emerging carbon sources, with important implications for the global climate. To investigate this trend, we analysed long-term census data from 49 forest sites spanning southeast and southern Brazil, including tropical and subtropical forests. We examined carbon dynamics and its relationship with tree diversity and functional traits that are tightly linked with species' carbon processing and storage capacities. Our findings reveal a long-term trend of taxonomic, functional and phylogenetic homogenisation and a decline in the forests' carbon sink. Specifically, homogeneous forests had lower carbon losses, whilst forests with more conservative species were associated with greater carbon gains and lower carbon losses. Overall, our study establishes a baseline to understand and predict the carbon sink in the face of ongoing climate change in this region.

Keywords: Carbon-diversity relationship; carbon sink; tropical forests; subtropical forests, dry forest; diversity decline; carbon sink decline; niche complementarity; mass-ratio.

Introduction

The effects of climate change on tropical forest carbon sequestration are complex. While the carbon sink of Amazon forests has been declining towards an expected zero in 2035¹, drier seasonal forests may have already turned into carbon sources². To fully understand these effects and predict future scenarios, we must consider the different ecological dimensions that affect carbon uptake, such as tree species diversity and functional trait composition^{3,4,5,6}. In the Amazon, some studies have found a positive effect of diversity on forest resilience to climate change^{7,4,8,9}. However, these relationships have been rarely explored on a comprehensive scale in other Brazilian forests, such as the Atlantic Forest¹⁰ (157,200 km²) and Caatinga dry forests¹¹ (850,000 km²), which experience lower water availability and different trait-productivity relationships^{12,13}.

Tree community responses to climatic oscillations and extreme weather events linked to climate change depend on the physiological reactions of trees to varying conditions of water availability and temperature^{9,1,14}. Lower rainfall and higher climatic water deficit (CWD) reduce the amount of water available for plant survival and growth, which may ultimately lead to reductions in forest carbon sinks and stocks^{15,9,14}. Plant responses to climate are also mediated by soil texture and fertility^{2,16}, with complex outcomes due to different responses in above- and below-ground biomass productivity¹⁷. Overall, higher nutrient availability, particularly of phosphorus, is expected to increase forest productivity^{16,17}. Temperature effects are also complex: while net productivity is positively correlated with temperature at the global scale¹⁸, climate change has been pushing tropical forests to critical temperature thresholds beyond which photosynthesis is impaired¹⁹.

Other than environmental factors, ecological aspects such as tree species diversity and functional trait composition also have an important role in carbon dynamics^{12,3,5,13}. Evidence points to diverse communities having higher resource-use efficiency due to niche complementarity effects^{20,21,22,14,24}. Over time and under fluctuating environmental conditions, these effects are hypothesized to result in stable carbon dynamics (i.e., ‘insurance hypothesis’)²³. Following this rationale, taxonomic diversity alone may not accurately reflect niche differentiation due to potential niche overlap among co-occurring species (i.e., functional redundancy)¹². Phylogenetic and functional diversity, on the other hand, may serve as better proxies for niche complementarity^{24,8}. In contrast, in less diverse communities where niche complementarity effects are minimal, the functional composition of the most abundant species may better predict community productivity (i.e., mass-ratio effects)²⁵. Although mass-ratio

effects operate in high-diversity communities²⁶, they have greater weight in low-diversity communities, reflecting the optimal traits that promote growth and survival in a given habitat¹².

Among these traits, specific leaf area (SLA) and wood density (WD) are often linked to forest productivity due to their role in tree survival and growth^{27,28,3,26,29,4}. They also help to identify underlying ecological strategies related to resource use and carbon assimilation in trees. Low WD and high SLA indicate an acquisitive strategy, usually linked to fast-growing and short-lived species with high carbon assimilation rates^{30,31,32,12,26}. Although acquisitive species may be vulnerable to hydraulic failure, stem breakage, and herbivory^{33,34,12,26}, many are able to endure high temperatures and low humidity by shedding their leaves during the dry season (i.e., deciduousness), particularly in nutrient-rich environments³⁵. Such adaptation could theoretically increase the survival of acquisitive deciduous species under a hotter and drier climate, despite evidence that tropical deciduous forests have had higher tree mortality than wetter forests in recent years². On the other end of the spectrum, high WD and low SLA indicate a conservative strategy, usually linked to slow-growing species less prone to hydraulic failure and carbon starvation^{31,36,12,38}. These conservative traits not only confer resilience to water-limited conditions, but also contribute to higher carbon stocks and productivity in such environments^{12,37}. In fact, because of climate change and increasing droughts, forests are likely to move towards a more conservative trait composition (functional homogeneity), resulting in lower taxonomic and phylogenetic diversity^{28,4,24}.

Here, we use an extensive and unique long-term dataset of 49 forest sites in south and southeast Brazil spanning up to 31 years of monitoring. We investigate the temporal trends of different facets of diversity and functional trait composition (hereafter, ‘ecological variables’) and their effects on forest carbon stocks and dynamics. We expect to find a trend towards a more conservative trait composition and, consequently, lower carbon productivity. We also expect to find higher and more stable carbon stocks and sinks in the most diverse forests compared to the least diverse forests due to complementarity-driven stability^{22,3,24}. At the same time, we acknowledge the possibility that the driest and least diverse forests of our dataset have been more stable over time, due to low SLA, high WD, deciduousness, and higher tolerance to drought and high temperatures. It should be highlighted, however, that it remains unresolved whether the species in these dry deciduous forests are currently at their physiological limits and, therefore, would be more vulnerable (not more resistant) to climate change^{38,2,19}.

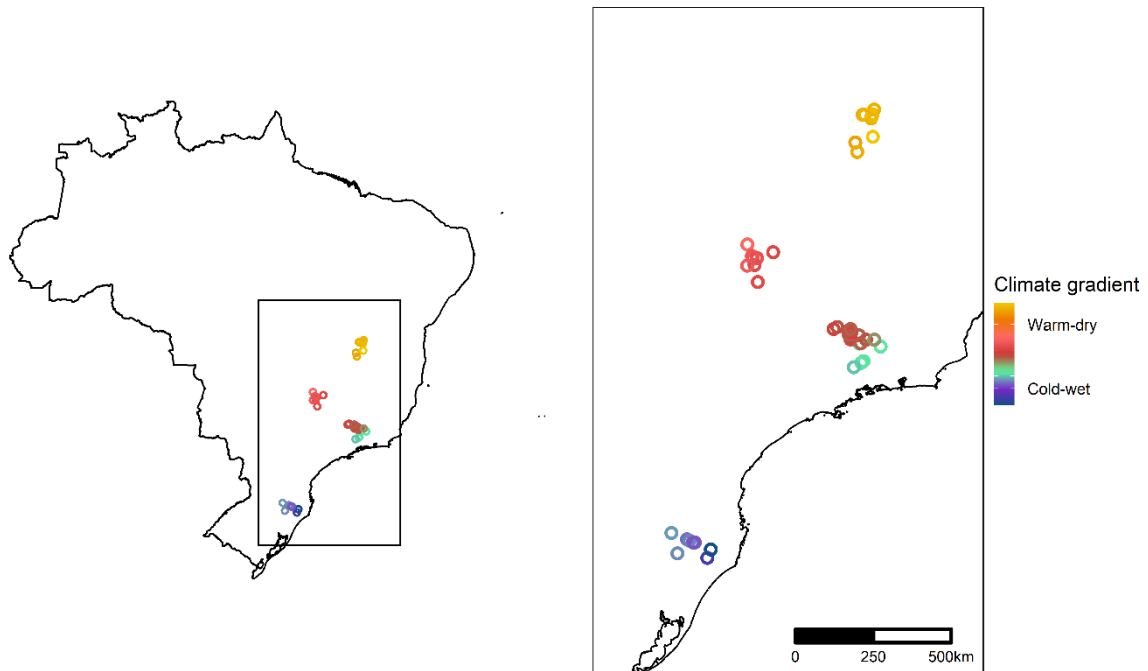


Figure 1. Spatial location of the sampled sites ($n = 49$) in Brazil. Points are coloured by the sites' climate (gradient obtained from PCA)

Results

Long-term trends

Our results showed that tropical and subtropical forests of south and southeast Brazil experienced climatic fluctuations throughout the study period (1987-2020). Overall, mean annual precipitation (MAP) and climatic water deficit (CWD) displayed a non-linear trend, while mean annual temperature (MAT) increased and drought peaks were observed in 2003 and 2015 (Figure S25). Carbon stocks across the sites generally increased until ~2013, when they began to decline (Table 1, Table S1, Figure 2A). The net carbon sink declined over time and reached zero in ~2013, driven by increasing carbon losses and decreasing carbon gains (Figure 2B-D, Figure S4). Meanwhile, the data showed an increase in carbon residence time (CRT) (Table 1, Figure 3D).

Table 1. Population-level predictions (average between sites at a given point in time) from the GAMs (Figures 2 and 3) for 2010 and 2020. Relative values are relative to the carbon stock of the site in the first year of the census interval.

	2010	2020
Carbon stocks (Mg C ha ⁻¹)	98.54	90.89
Net carbon sink (Mg C ha ⁻¹ yr ⁻¹)	0.788	-2.059
Net carbon sink (relative)	0.009	-0.021
Carbon gains (Mg C ha ⁻¹ yr ⁻¹)	2.427	1.643
Carbon gains (relative)	0.025	0.017
Carbon losses (Mg C ha ⁻¹ yr ⁻¹)	1.65	3.362
Carbon losses (relative)	0.017	0.043
Carbon residence time (years)	41.56	53.14

Although taxonomic diversity remained stable before starting to decline in ~2005-2010, we observed a long-term decline in phylogenetic diversity (Table S1, Figure 4A-B). Similarly, although specific leaf area (SLA) showed a positive trend until ~2010, after which it stabilised, SLA dispersion decreased linearly over time (Table S1, Figure 4C-D). WD was mostly stable (and even slightly increasing) until about 2012, when it started to decline (Table S1, Figure 4E). At the same time, WD dispersion, which showed a negative trend until about 2012, started to increase (Table S1, Figure 4F).

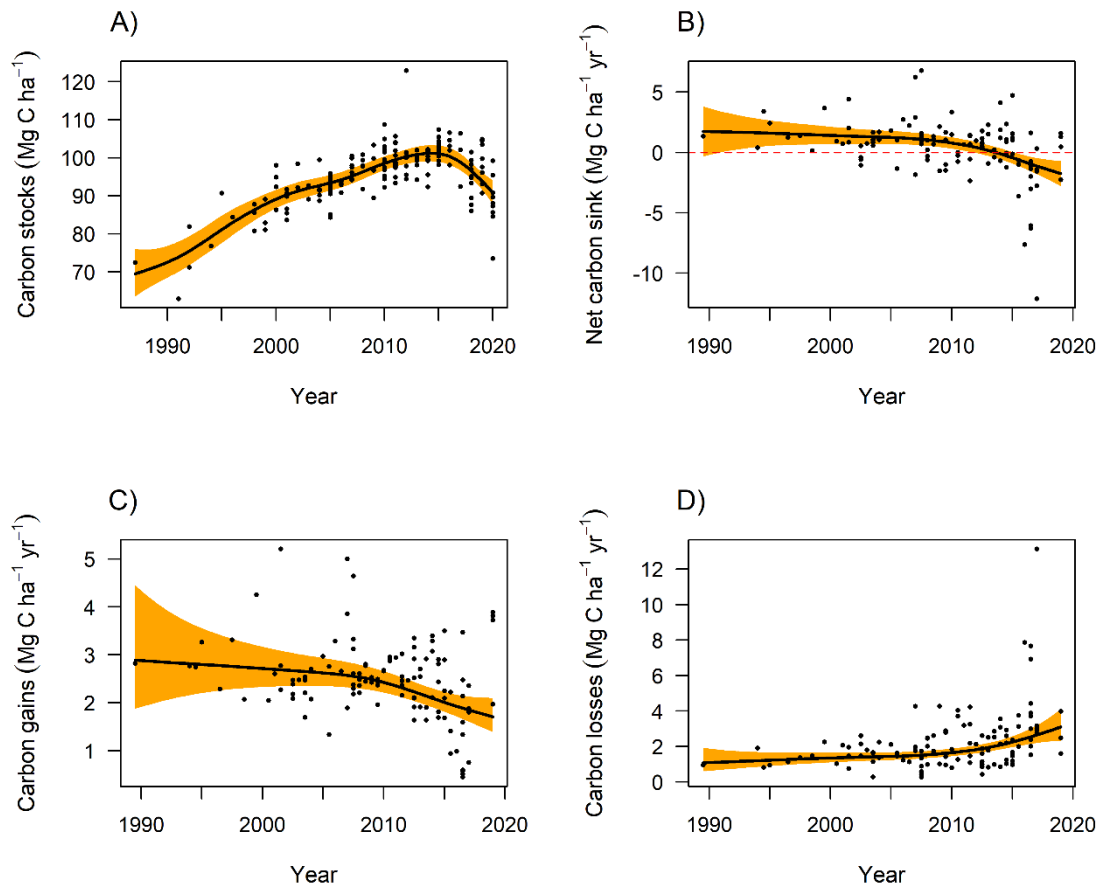


Figure 2. Long-term trends of carbon dynamics variables. Curves are smooth splines fitted with generalized additive models (GAM). Points are partial residuals (after accounting for the random effect of sites, $n = 49$), corresponding to each census for carbon stocks ($n = 163$) and to each census interval ($n = 114$) for the carbon dynamics variables. Shaded areas represent 95% confidence intervals. Smooth curves with coloured shades were significant at a 95% confidence level.

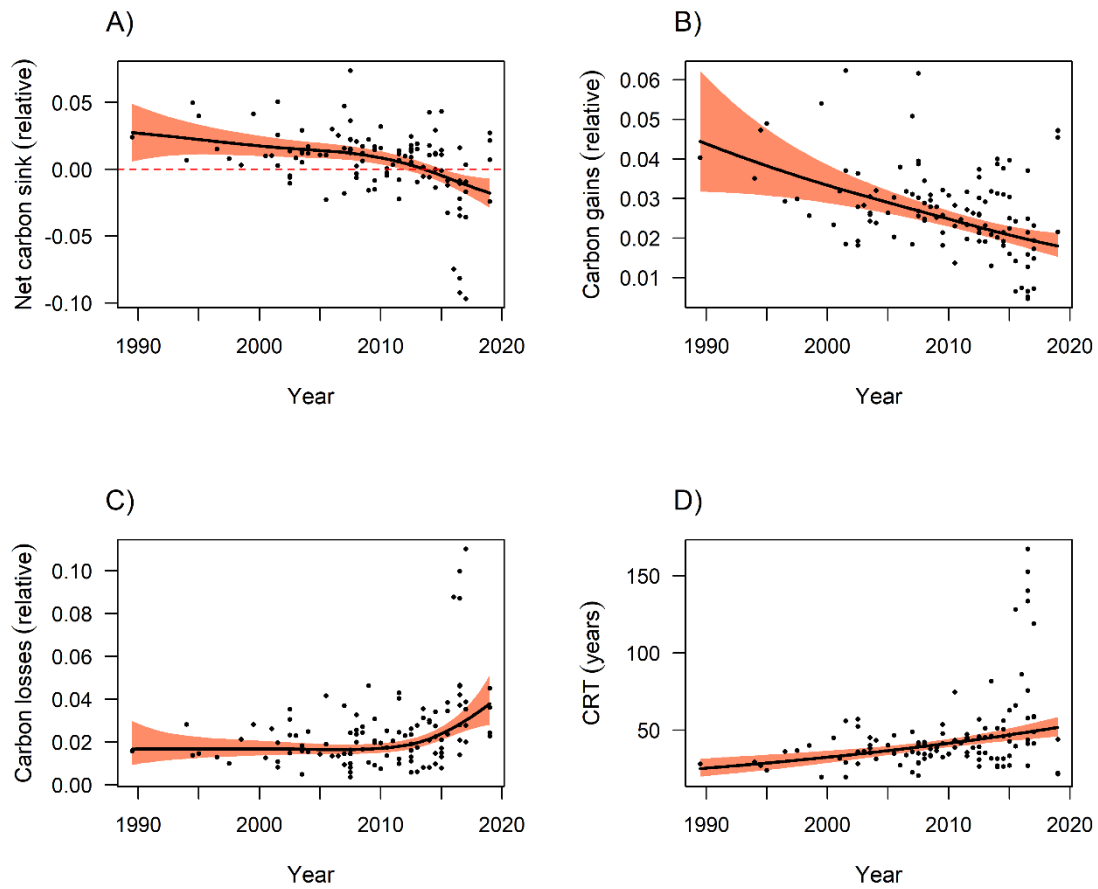


Figure 3. Long-term trends of the relative (to carbon stocks) values of carbon dynamics variables and carbon residence time (CRT). Curves are smooth splines fitted with generalized additive models (GAM). Points are partial residuals (after accounting for the random effect of sites, $n = 49$), corresponding to each census interval ($n = 114$). Shaded areas represent 95% confidence intervals. Smooth curves with coloured shades were significant at a 95% confidence level.

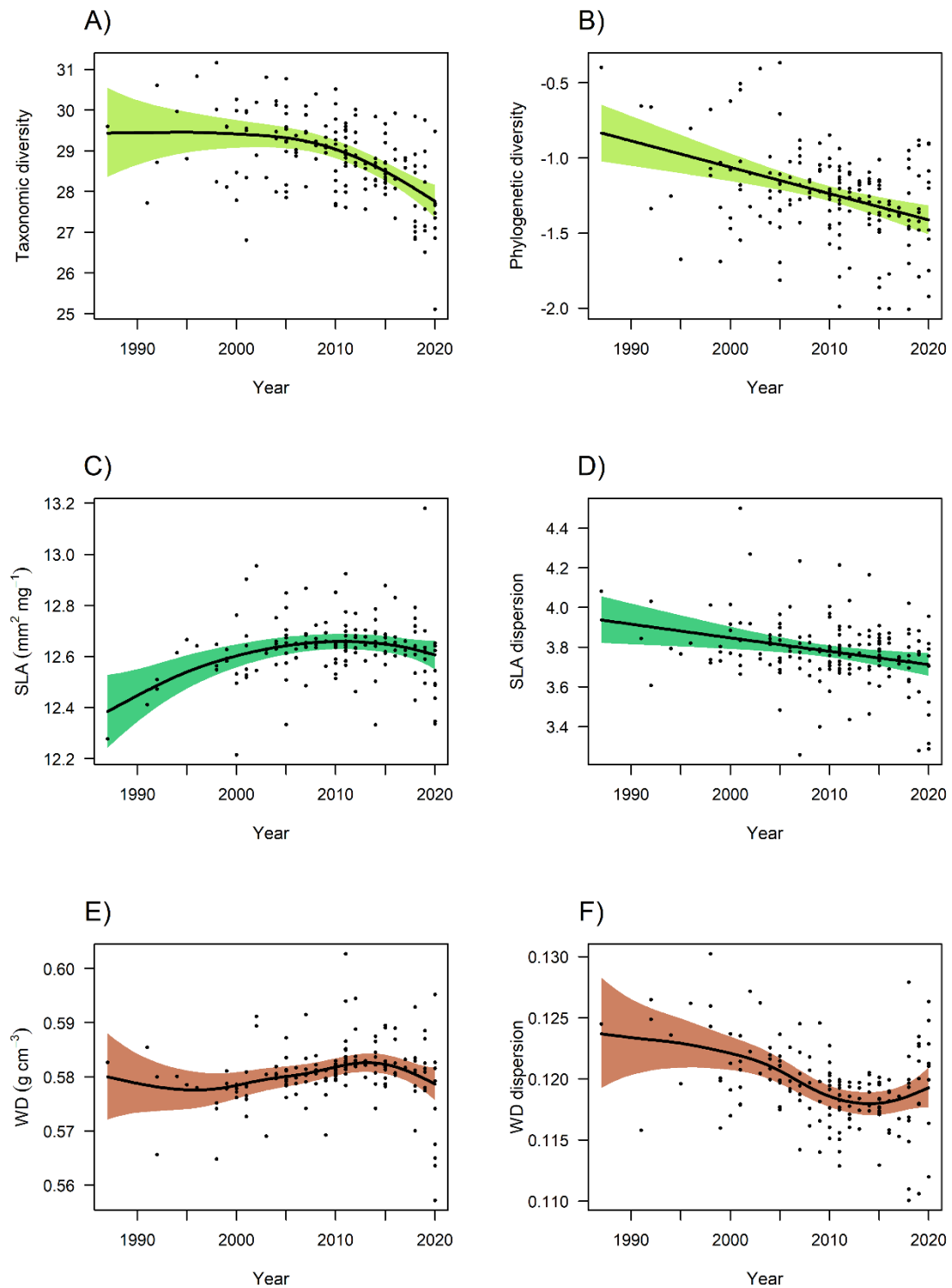


Figure 4. Long-term trends of taxonomic and phylogenetic diversity, functional trait community weighted means and functional trait weighted coefficient of variation (dispersion). Curves are smooth splines fitted with generalized additive models (GAM). Points are partial residuals (after accounting for the random effect of sites, $n = 49$) corresponding to each census ($n = 163$). Shaded areas represent 95% confidence bands intervals. Smooth curves with coloured shades were significant at a 95% confidence level.

Carbon and climate relationships over time

The direction of the relationship between each carbon variable and time varied. Carbon stocks, losses, relative carbon losses and carbon residence time (CRT) had a positive relationship with time, whereas net carbon sink, relative net carbon sink and relative carbon gains had a negative relationship with time (Figures 5-6, Figures S26 and S27). The interaction between time and climate revealed that the warmest-driest sites had the steepest decline in net carbon sink, due to the increasing carbon losses over time (Figures 5 and 6, Figures S26 and S27). The increases in CRT were more pronounced in the warmest-driest sites, while the CRT of the coldest-wettest sites showed a stable trend (Figure 6, S14D).

In general, warm-dry sites had lower carbon stocks and gains than cold-wet sites, although they showed similar values for net carbon sink, carbon losses and all relativised variables (Figures 5 and 6, Figures S13 and S14). Because of the interaction between climate and time, we found that the warmest-driest sites trended in recent years towards a lower net carbon sink and relative net carbon sink, which were associated with lower relative carbon gains and higher carbon losses, relative carbon losses and CRT (Figures 5 and 6, Figures S26 and S27). Thus, the relationships between climate and carbon dynamics became more pronounced over time because of the decreasing net carbon sink of the warmest-driest sites (Figures 5 and 6, Figures S26 and S27).

Carbon and soil relationships

We found a negative relationship between the phosphorus-to-magnesium PCA axis and carbon stocks and gains (Figures 5 and 6). This means that the phosphorus-rich and magnesium-poor forests seemed to have large and increasing carbon stocks. Soil fertility had a positive relationship with net carbon sink, relative net carbon sink, carbon gains and relative carbon gains, although the latter had $P = 0.054$. The aluminium-phosphorus PCA axis, which was positively related to both aluminium and phosphorus contents, had a negative relationship with both absolute and relative carbon gains and a positive relationship with CRT.

Carbon and ecological variables relationships

We analysed the relationships between carbon and ecological variables with and without interactions with year. Excluding interactions, WD was positively linked to absolute and

relative values of net carbon sink and gains and negatively linked to carbon losses and CRT. SLA was positively linked to carbon losses and CRT and negatively linked to relative net carbon sink and relative carbon gains. Finally, phylogenetic diversity (PD) was only positively linked to carbon gains (Figures 5 and 6). Including interactions, forests with high WD dispersion showed a stable (rather than an increasing) carbon stock trend and high rates of both absolute and relative carbon loss. In contrast, forests with low WD dispersion showed higher carbon stocks in recent years and lower carbon losses (Figures 5-7). We also detected a modest interaction between PD and year on carbon stocks, suggesting that forests with higher PD may have experienced a greater rate of carbon stock increase over time compared to those with lower PD (Figures 7-9).

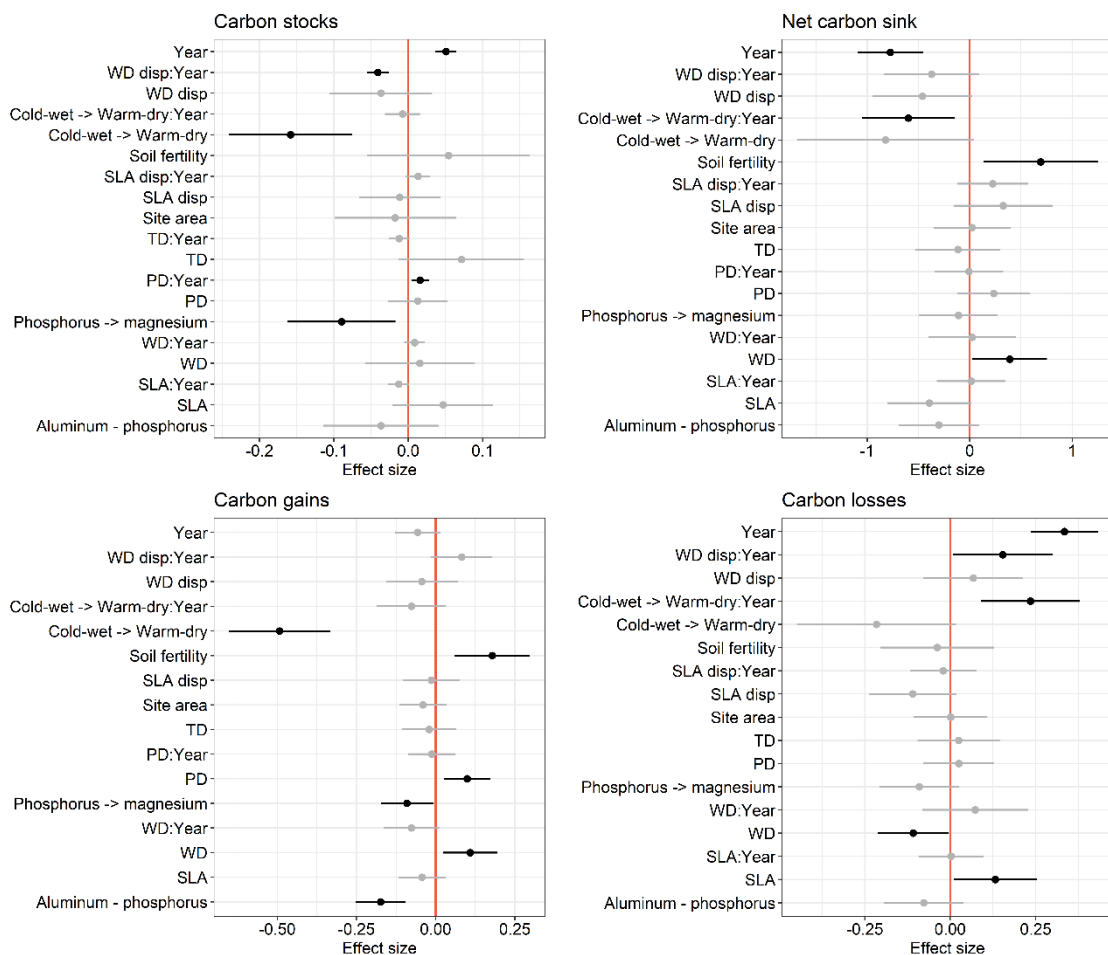


Figure 5. Conditional average coefficients for the selected models ($\Delta AIC_c \leq 4$) for carbon stock, net carbon sink, carbon gains and carbon losses. All models included the effects of time, climate, soil, diversity and functional traits composition. The variance explained (marginal R^2) by the best model was 29.7% for carbon stocks, 33.1% for net carbon sink, 47.1% for carbon gains, and 28.6% for carbon losses. For each variable in the model, dots represent conditional averaged coefficients with their 95% confidence intervals; the coefficients and

confidence intervals of variables not included in the averaged model were set to zero. For carbon stocks we used censuses ($n = 163$) nested within sites ($n = 49$); and for the net carbon sink, carbon gains and carbon losses, we used census intervals ($n = 114$) nested within sites ($n = 49$). Coefficients were estimated using linear mixed-effects models (LMM, including a random effect of site). The coefficients of the carbon stocks were estimated with carbon stocks in the logarithmic scale and all models were fitted with scaled predictors.

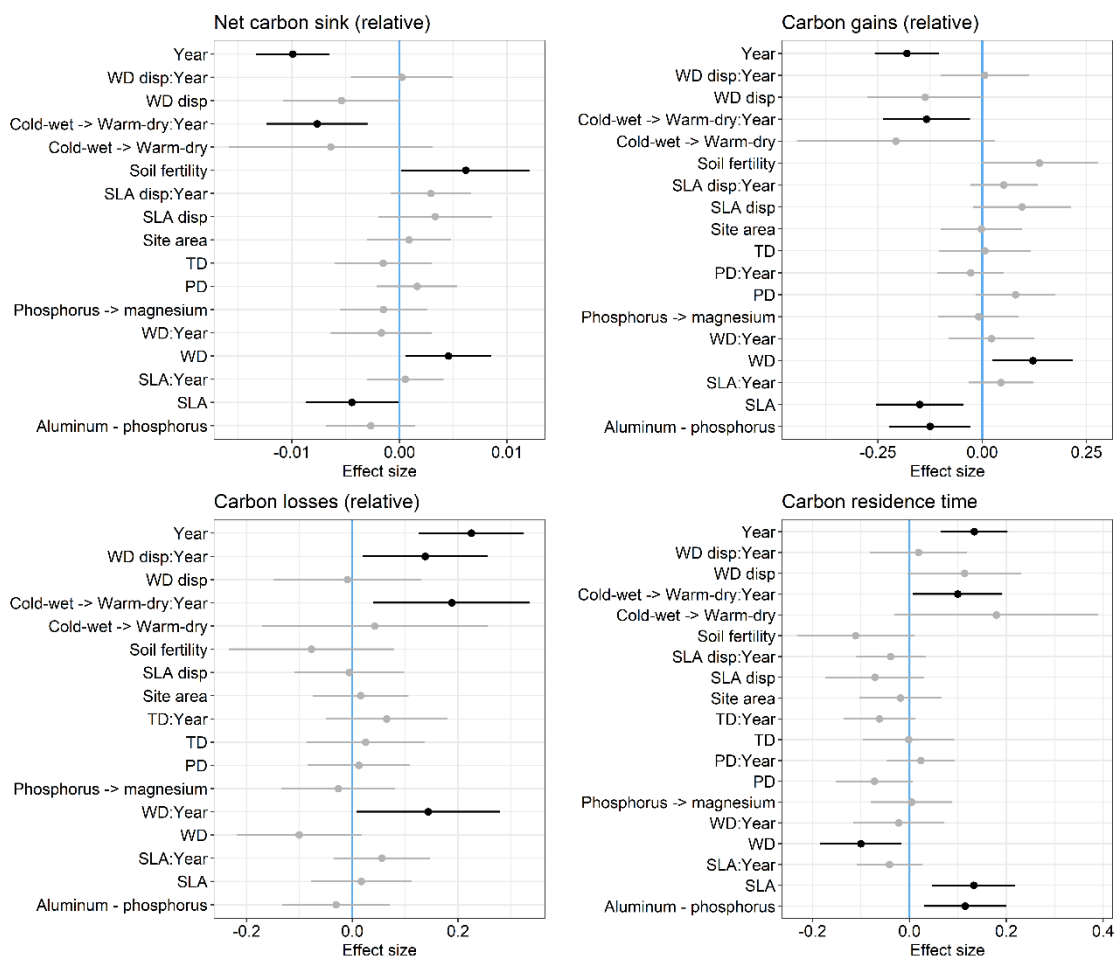


Figure 6. Conditional average coefficients for the selected models ($\Delta AIC_c \leq 4$) for relative net carbon sink, relative carbon gains, relative carbon losses and carbon residence time. All models included the effects of time, climate, soil, diversity and functional traits composition. The variance explained (marginal R^2) by the best model was 34.7% for relative net carbon sink, 39.2% for relative carbon gains, 18.3% for relative carbon losses, and 33.6% for carbon residence time. For each variable in the model dots represent the conditional averaged coefficients with their 95% confidence intervals; the coefficients and confidence intervals of variables not included in the averaged model were set to zero. We used census intervals ($n = 114$) nested within sites ($n = 49$). Coefficients were estimated using linear mixed-effects models (LMM, including a random effect of site). The coefficients were estimated with the response variables in the logarithmic scale and (except relative net carbon sink) all models were fitted with scaled predictors.

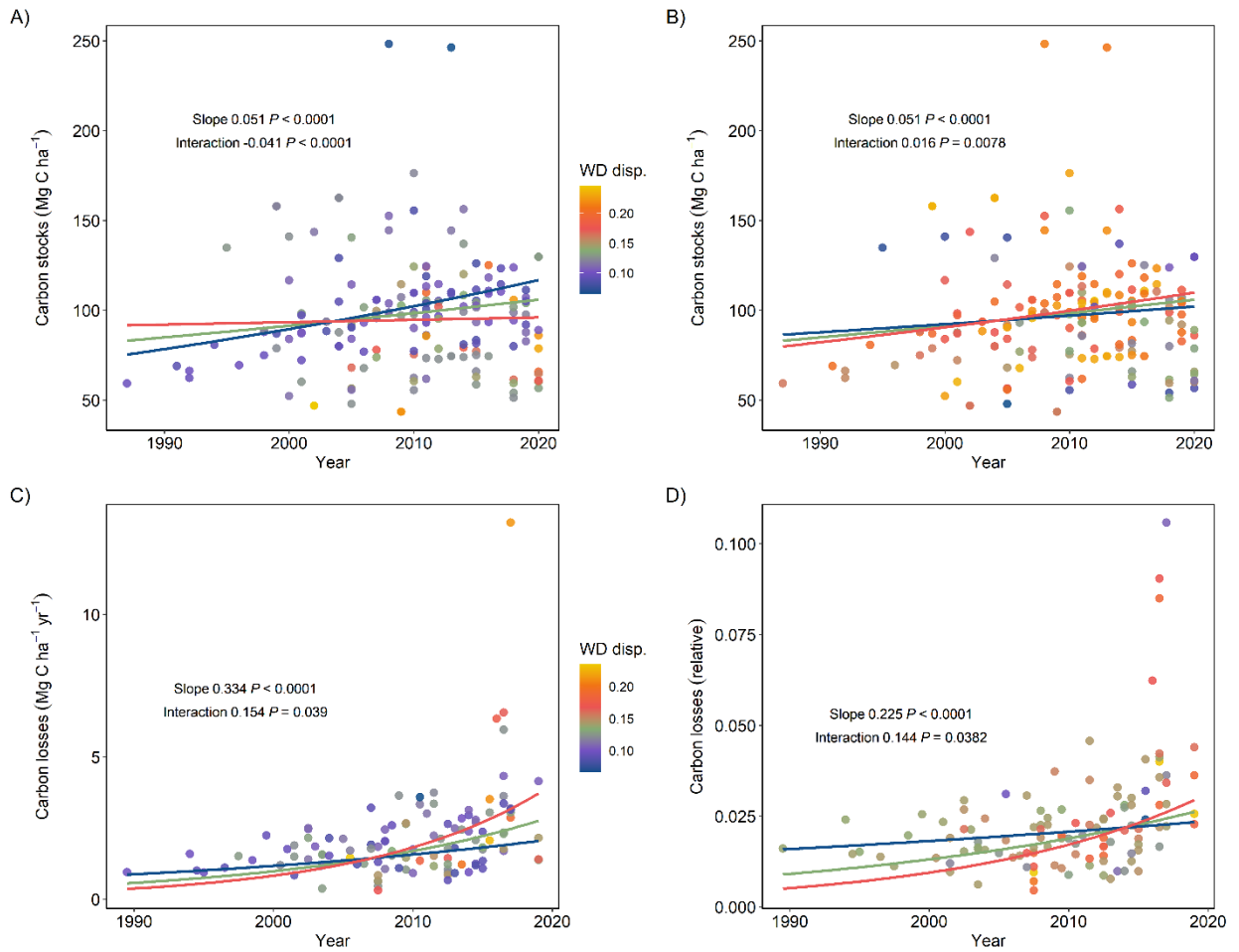


Figure 7. Long-term trends of carbon stocks (A, B), carbon losses (C) and relative carbon losses (D) on varying levels of A) WD dispersion, B) phylogenetic diversity, C) WD dispersion and D) WD community weighted mean. Points are raw residuals and the curves were fitted with linear mixed-effects models (LMM, including a random effect of site; same models described in figures 5 and 6).

Discussion

Long-term trends of carbon dynamics and diversity

Forests with negative net carbon sinks (i.e., carbon sources) are widespread across the entire sampled climate space. Although the coldest-wettest sites had higher carbon uptake and stocks *per* year when compared with the driest-warmest sites, most are transitioning from net carbon sinks to net carbon sources over time². We also found that both diversity and mass-ratio mechanisms may simultaneously drive carbon dynamics, with context-dependent effects.

We found a long-term decline in taxonomic, functional, and phylogenetic diversity (Figure 4). These results indicate functional homogenisation of Brazilian tropical and subtropical forests driven by climate change^{28,24}. Functionally, these forests have shifted during most of the monitoring period towards a narrower range of specific leaf area (SLA) and wood density (WD). Although the direct drivers of this homogenisation are difficult to assess and we have not delved into these aspects, recent literature suggests that drought and rising temperatures are likely to be the most important drivers^{28,39,24}. Although disturbance and forest age are expected to be spatially homogeneous in our samples based on the sampling criteria and historical data, successional processes cannot be completely disregarded. Thus, considering that successional processes are controlled in our samples, diversity and carbon losses can be a result of physiologically driven tree mortality²⁸. In fact, with more trees dying because of physiological responses to climate fluctuations, certain species, traits, and lineages, particularly the ones with narrower niches, are more likely to disappear from a given community⁴⁰. Conversely, rare species inhabiting non-optimal environments might benefit from climate change if the emerging conditions align more closely with their niche requirements.

Both functional trait variables assessed (SLA and WD) showed subtle fluctuations over time. The WD trend changed from slight positive to negative in ~2012, coinciding with the change in the WD dispersion trend, which started to increase around the same time. These shifts also coincided with the period when the forests shifted from carbon sinks to carbon sources. It is possible that the carbon sink decline was associated with the death of large individuals from high-WD species, which decreased the average WD of the communities. Because high-WD species are less prone to cavitation and usually perform better under water-limited conditions, one could expect an increasing WD trend in forests experiencing climate change effects^{12,28}. However, our results contradict this expectation by showing that, temporally, the carbon sink decline seemed associated with the death of individuals from conservative high-WD species. Moreover, although SLA was more stable than WD after 2012, it showed a slight decrease thereon, while SLA dispersion showed an almost linear decrease throughout the monitoring period.

Overall, these results may suggest two paths in the functional composition trends of our sites. First, a growing frequency of thicker leaves and less dense wood in the forest community could indicate an increasingly conservative strategy at the leaf-trait level and an increasingly acquisitive strategy at the wood-trait level. Alternatively, if such trends are no more than oscillations, both wood and leaf traits could remain stable around the values they have reached in the last decades (Figure 4). However, carbon losses were associated with lower WD and

higher SLA, indicating acquisitive strategies over time (i.e., no interactions between time and the community-weighted means of WD and SLA). This relationship was not affected by the shift that occurred around 2012. Although our results do not reveal the direct drivers of the diversity decline, these trends suggest that even in the absence of deforestation, species and lineage losses are likely to occur at a substantial rate due to climate change³⁹. Strong climate change effects are expected to be seen in the Amazon in the next years³⁹; however, in forests that already have lower diversity and biomass and are under more limiting environmental conditions, strong climate change effects may have already started^{38,2}.

The difference between the net carbon sink of the warmest-driest sites and that of the coldest-wettest sites has increased in the last few decades². Due to greater carbon losses over time, the net carbon sink of the driest forests was smaller than that of the wettest forests². Therefore, the carbon stock differences between the driest and the wettest sites have increased, while the carbon stocks of the wettest sites have remained the greatest. In contrast with Maia et al. 2020², the relationship between time (and its interaction with climate) and carbon gains was not statistically significant in our full model, revealing that the carbon sink decline is more likely to be caused by the increasing carbon losses. However, the relative carbon gains declined over time, with the most pronounced decline observed among the warmest-driest sites. This result indicates increasing tree growth limitation in the warmest-driest sites, further reinforcing their vulnerability to climate change. The CRT of the warmest-driest sites has experienced a long-term increase and is currently greater than that of the coldest-wettest sites. The decreasing carbon gains of the warmest-driest sites are likely driving the CRT increases because $CRT = \text{carbon stocks} / \text{carbon gains}$. These patterns were also found in Maia et al. (2020)² (except for relative values and CRT, which were not included in the 2020 study), which used 32 sites of the 49 used in this study. Expanding the latitudinal and longitudinal gradients of the previous study did not change these results, indicating that the subtropical forests of south Brazil and the semideciduous forests of central Brazil are probably following a similar trend.

Environmental and ecological drivers of carbon dynamics

Both the phosphorus-to-magnesium and aluminium-phosphorus axes of the soil PCA had negative relationships with carbon gains. In other words, carbon gains were generally lower in aluminium-rich and magnesium-poor forests, although the relationship with phosphorus showed conflicting trends depending on the soil fertility axis considered. Here, we interpret these results considering that carbon gains are likely to decrease with aluminium and increase

with phosphorus, for the following reasons: (i) the contribution of phosphorus in the aluminium-phosphorus component is smaller than that of aluminium, (ii) the contribution of phosphorus in the phosphorus-to-magnesium component is greater than that of magnesium, and (iii) phosphorus-to-magnesium had a negative relationship with carbon stocks. These findings are consistent with the negative effects of aluminium toxicity and the positive effects of soil phosphorus availability on tree growth^{41,42,43,44}. For relative carbon gains, only a relationship with aluminium-phosphorus was detected, further indicating the detrimental effect of aluminium toxicity for tree growth in these forests. The positive relationship between aluminium-phosphorus and CRT probably owes to the relationship between CRT and carbon gains ($\text{CRT} = \text{carbon stocks} / \text{carbon gains}$). The potential negative relationship between magnesium and carbon stocks and gains should be further investigated. However, as the contribution of magnesium to the phosphorus-to-magnesium axis was smaller than the contribution of phosphorus, these relationships are probably more associated with phosphorus than magnesium. Moreover, we also found that the net carbon sink, relative net carbon sink and carbon gains increased with soil fertility, as expected considering that low nutrient availability limits plant growth^{45,46}. This finding highlights the confounding effects of soil and climate on this region's carbon dynamics, because the warmest-driest sites (deciduous forests) contain the most fertile soils due to slower nutrient leaching⁴⁷. Therefore, as expected, deciduous forests' lower carbon stock and sink are probably related to climate.

Carbon gains increased with phylogenetic diversity (Figure 4B) and the temporal increases in carbon stocks were slightly more pronounced in sites with higher phylogenetic diversity than in sites with lower phylogenetic diversity (Figures 4B and 7B). Since the phylogenetic relationships among species tend to predict functional similarity to a certain extent^{24,8}, the effect of PD on carbon gains is consistent with niche complementarity effects and recent findings on carbon-diversity relations in tropical forests⁶. Therefore, because we already accounted for SLA dispersion and WD dispersion, niche complementarity could be related to other factors, as follows. (i) The portions of SLA and WD not captured by our data, (ii) unmeasured traits involved in carbon processing and storage (e.g., root, stem and leaf physiology and canopy architecture^{24,8}) and/or (iii) the lower vulnerability of distantly related species to similar pathogens due to pathogen dilution effects⁴⁸.

Forests with higher WD dispersion showed the most pronounced increases in both absolute and relative carbon losses, while their carbon stocks remained relatively stable over time – unlike the general trend of increasing carbon stocks (Figs. 6-7). These relationships likely reflect the negative relationships between WD dispersion and net carbon sink and relative net

carbon sink, which had small, although non-statistically significant, P-values ($P = 0.07$; Figures 5-6, Table S3 and S4. This indicates that trees with WD values approaching the community's extremes are being eliminated, given the decreasing tendency of WD dispersion (Figure 4F). On the other hand, the carbon losses suffered by forest communities with a narrower WD range was mostly stable over time, suggesting resilience to climatic fluctuations. At the same time, WD was positively linked to net carbon sink and carbon gains (and their relativised values) and negatively linked to carbon losses and relative carbon losses, although the latter was not statistically clear ($P < 0.1$). Meanwhile, WD had a negative effect on CRT, which can be related to its positive effect on carbon gains. Although one could argue that the positive relationship between WD and carbon gains and net carbon sink is biased by the use of WD in the calculation of AGWB, our results suggest that high WD has been consistently linked to tree survival and growth throughout the monitoring period. This is further supported by the observation that the relative values of these metrics also showed a positive relationship with WD. In addition, as carbon stocks – though often expected to be influenced by WD – were not affected, and a negative relationship was observed with carbon losses, contrary to expectations of a positive one. These results indicate that the observed relationships are unlikely to be an artefact of WD-based calculations. However, we have also observed an increasing trend of relative carbon losses over time, regardless of community WD. Since the relationships between WD and carbon gains and between WD and net carbon sink have remained stable over time, this suggests that the typical pattern of high WD predicting a high carbon sink may shift in the future.

The relationship between WD and SLA with carbon variables suggests that forests with a predominance of softer leaves and lighter wood have been the most vulnerable. High-SLA forests (i.e., with softer leaves) had the greatest carbon losses and the lowest relative carbon sinks and relative carbon gains in our dataset. This pattern is not likely to have changed over time since no statistically clear interactions between SLA and time were detected. These findings are consistent with the hypothesis that, despite faster turnover among acquisitive species, acquisitive traits predict higher vulnerability under limiting environmental conditions, such as during drought events^{12,26}. For example, high SLA is typically linked to high respiration and transpiration rates, which may impair growth and survival during drought periods^{31,12,26}. Conversely, low SLA (i.e., thicker leaves) enables plant functioning to persist even at reduced leaf water potentials during dry periods¹². Therefore, our findings reinforce that, under limiting conditions, conservative traits are more associated with growth and survival than acquisitive traits^{12,28,26}. Thus, although acquisitive traits are typically linked to higher growth rates and

faster turnover, they are also linked to higher mortality, competition, vulnerability to drought-induced cavitation and temperature-induced water loss^{12,33,34,26}. At the same time, SLA was positively linked to CRT, indicating that carbon tends to persist longer in forests with higher SLA (i.e., softer leaves). Combined with the observation of higher CRT in low-WD forests, this indicates that forests characterised by acquisitive SLA and WD composition may retain carbon for longer periods. However, given the long-term increase in carbon stocks followed by a recent decline over the last 10 years, these patterns may shift as carbon stocks stabilise in the future^{12,28}.

Final remarks

Our results showed that Brazilian tropical seasonal forests and subtropical evergreen forests have experienced a decline in tree diversity and carbon sink. The relationships between carbon dynamics and diversity seem to be context-dependent: while phylogenetic diversity predicted higher carbon gains, trait diversity (particularly wood density) predicted higher carbon losses over time. We also found that forests composed of mostly conservative species (i.e., denser wood and thicker leaves) tend to show higher productivity. We recognise the limitations of the data, especially related to the phylogenetic and functional variables and the application of complex (and less generalisable) models for data exploration and hypothesis testing. We also acknowledge the need for precise measures of disturbance history and forest age to better understand the carbon sink dynamics in these regions. However, our sampling strategy was designed to represent the most conserved and least disturbed forests, so disturbance and age are unlikely to confound the observed relationships. This supports the reliability of our findings, although the role of disturbance in these forests warrants further investigation. In addition, as our samples are spatially clustered, caution is needed when extrapolating our conclusions to the regions between the large-scale clusters.

Our evidence suggests that conservation policies that do not take carbon-diversity relationships into account may be less effective. Therefore, to jointly safeguard different facets of forest diversity and preserve forest carbon sinks, carbon-diversity relationships should be considered. These are also useful for restoration planning and for predicting the vulnerability and resilience of these forests in the near future. In addition, these results have relevant implications for the conservation of ecosystem services, which can be extended to other forests in south and southeast Brazil. Our target sites have been protected from anthropogenic disturbances and monitored for decades, which sets them apart from most forests in the region,

largely neglected by conservation efforts. Consequently, the concerning trends observed in carbon sink and biodiversity reduction in this study may be even worse in less conserved forests, leading to more severe consequences for ecosystem services.

Materials and methods

Study design

We used data from 49 repeatedly measured forest sites in Brazil, characterized as deciduous, semideciduous, and evergreen forests (Supplementary File 1; data of 32 sites were used in Maia et al. 2020²). The sites are located in tropical and subtropical regions across south and southeast Brazil, spanning the latitudes 28° 19' S to 14° 16' S (Figure 1). The mean annual temperature (MAT), mean annual precipitation (MAP) and mean altitude of the sites were, respectively, 20.6 °C (from 13.3 to 25.2 °C), 1450 mm (from 669 to 1998 mm) and 900 m a.s.l. (from 450 to 1536 m a.s.l.). Altitude is negatively correlated with MAT across the sites ($r = -0.84$). Both MAT and MAP follow a latitudinal gradient, with MAT increasing and MAP decreasing northward (Figure S1). The driest and warmest forests in our gradient (tropical dry deciduous) are established on fertile soils in the northernmost sites, while the coldest and wettest forests in our gradient (subtropical and tropical evergreen) are established on soils of varying fertility but generally poorer in the southernmost sites. The semideciduous forests experience an intermediate climate in the tropical region. The minimum distance between sites is ~1 km and the maximum distance is > 1000 km.

The 49 forest sites are distributed across four spatial clusters (Figure 1), which are strongly correlated with climate. Despite substantial within-cluster climate variation, we achieved 100% accuracy when using climatic variables to predict the cluster assignment of each site. Sites within the same cluster have an average maximum distance of ~150 km and an average distance of ~60 km. Such distribution characterises large-scale variations (between clusters) and regional variations (within clusters). Despite the spatial proximity between some of the sites (< 5 km), there is high local-scale environmental heterogeneity within the clusters, driven by soil, topography and proximity to rivers and streams. Hence, we can assume independence between the sites, since their climatic and compositional similarities will have been incorporated by the model predictors (i.e., climate and functional composition).

The sites were selected to represent forests at advanced successional stages with minimal human intervention. Although we were unable to determine the exact age of each

forest, we conservatively estimate that they are likely over 50 years old. Based on field observations and personal communication with reserve managers, local communities and landowners, the sites have not experienced the effects of fire, landslides, floods or logging during or before the monitoring period. Thus, disturbance history and forest age are not expected to be correlated with space and environmental conditions.

Site area ranged from 3.4 to 1179 ha (mean of 112 ha), sampled with multiple subplots of 400 m² (in most sites). The area sampled in each site ranged from 0.2 to 5 ha (mean of 1.03 ha), totalling 50.4 ha across all sites. Although most subplots were located in forest interiors, edges were also captured, since sampling was designed to cover within-site heterogeneity in most cases. The number of censuses *per* site ranged from 2 to 8 (mean 3) and the total monitoring length, from 1 to 31 years (mean 11 years) (Figure S1). The length of the census intervals, between 1 and 9 years (mean 5 years), varied among the sites and within the same site over time (Figure S1). Forest census data is hosted in the ForestPlots.net platform (<https://www.forestplots.net>).

Tree vegetation sampling

In each census, we measured all trees with a quadratic mean diameter at 1.3 m (qDBH) ≥ 5 cm. This approach enables the inclusion of multi-stemmed trees with slender stems ($d < 5$ cm) if their quadratic mean diameter reaches 5 cm⁴⁹, following the operation: $qDBH = \sqrt{(d_1^2 + d_2^2 + \dots + d_n^2)}$; where d is the diameter at 1.3 m of each stem of a given tree. A different inclusion criterion was used in eight semideciduous forest sites, in which multi-stemmed trees were included if at least one of their stems had a diameter at breast height (DBH) ≥ 5 cm. The height of the point of measurement (POM) was marked in each stem and used as a reference for the ensuing censuses in most sites. See Figures S2 and S3 for site-specific DBH and qDBH distributions. Taxonomic nomenclature was based on Angiosperm Phylogeny Group IV (APG IV 2016)⁵⁰ and standardised using the R package *flora*⁵², following *Flora do Brasil 2020*⁵¹. We dropped Arecaceae, Dicksoniaceae, Cyatheaceae, and Cactaceae (~1% of the stems) to avoid biases in biomass calculation.

Carbon stocks and dynamics

To calculate above-ground woody biomass (AGWB), we extracted wood density values (WDi) from the Global Wood Density Database, the published literature, and field collections

(details in the '*Functional traits and functional diversity*' section). We used the modified pantropical allometric equation of Chave et al. (2009)³² through the R package *BIOMASS*⁵³. This equation has parameters for DBH, WDi and environmental stress (E), which is used to estimate tree height. We alternatively considered using a height-diameter allometric equation to estimate heights. However, we decided against this approach because the biomass estimated from this equation was more correlated with the climate variables than the biomass estimated from using the E parameter in the modified pantropical allometric equation. We converted the AGWB estimates to above-ground carbon (AGWC) by multiplying AGWB by 0.456⁵⁴. Carbon stocks (Mg C ha⁻¹) were estimated for each site in each census by summing the AGWC of each living tree and scaling the result to a per-hectare basis. To estimate carbon gains (Mg C ha⁻¹ yr⁻¹), we first summed the AGWC represented by the growth of each surviving tree (captured by changes in DBH) and the AGWC of newly recruited trees (those that reached 5 cm DBH or qDBH from one census to the next). Recruits were assumed to have DBH = 0 at the start of the interval⁵⁵. Then, the carbon gains were divided by the census interval length (in years) and scaled to a per-hectare basis. Carbon losses (Mg C ha⁻¹ yr⁻¹) were calculated as the sum of the AGWC of the trees and stems that died during the interval divided by the interval length and scaled to a per-hectare basis. We corrected the carbon gains and carbon losses using the equation CIC_1 proposed by Talbot et al. (2014)⁵⁵ to deal with the bias caused by census interval length. We applied this correction because larger census intervals can underestimate productivity, therefore, a small value, which is proportional to the interval length, is added to the observed values⁵⁵. Net carbon sink (Mg C ha⁻¹ yr⁻¹) was calculated as carbon gains minus carbon losses. We also calculated the relative values of (%) carbon gains, carbon losses and net carbon sink by dividing each one by the carbon stocks of the start of the census interval. Carbon residence time (CRT, in years) was calculated as carbon stocks divided by carbon gains^{1,14}. Census interval length was calculated as the difference between the end and start years of each interval, using decimal years to account for months. For the subsequent forest dynamics analyses (carbon gains, carbon losses, and net carbon sink), we used the midpoint year of each interval, calculated as the average of the end and start years and rounded to the nearest year. Carbon stock estimates were based on census-level data, while analyses of forest and carbon dynamics were based on census-interval data.

Taxonomic diversity

We used the effective number of species (Hill numbers) to represent tree taxonomic diversity⁵⁶. To account for uneven sampling efforts across the sites, we used the R package *iNEXT*^{56,57}, applying coverage-based rarefaction and extrapolation assuming 90% of sample completeness. For each census at each site, we calculated rarefied/extrapolated Hill numbers for species richness ($q = 0$), the exponential of Shannon's entropy index ($q = 1$), and the inverse of Simpson's concentration index ($q = 2$). However, due to strong correlations among these metrics ($r > 0.9$; Figure S5), we retained only Shannon diversity for further analyses. Hence, to represent taxonomic diversity during each census interval, we used the midpoint value of Shannon diversity, calculated as the mean of the start and end census values.

Functional traits and functional diversity

We extracted most wood density values (WD, g cm^{-3}) from the Global Wood Density Database^{32,58} and the published literature^{59,60,61,62,63}. For 7.9% of the species and 16.3% of the basal area in our dataset, we used field-collected WD values. Similarly, specific leaf area (SLA, $\text{mm}^2 \text{mg}^{-1}$) was obtained from the literature^{59,60,61,62,64,63,12,65} and field-collected data. The latter represented 27.5% of the species and 64.2% of the total basal area in our dataset. Species names in all data sources were standardized as per *Flora do Brasil 2020*¹² to maximize matches with our dataset. The field collection and trait measurements followed the standard protocol proposed by Pérez-Harguindeguy et al. (2013)⁶⁶. When trait values were not available for a given species in our dataset, we used the average trait value of other species in its genus or family. When the same trait was available at the species level in more than one source, we used the average of the available values. On average across all censuses, the individuals for which we used species-level WD and SLA represented $61.7\% \pm 17.7\%$ and $76.7\% \pm 18.8\%$ of the carbon stocks, respectively (mean $\pm$ SD). Genus-level data were used for 27.3% of the carbon stocks for WD and 16.14% for SLA, while family-level data accounted for 10.5% and 5.6%, respectively (Figures S6 and S7). Although the practical difficulties of massive trait data collection in the field render the use of average traits from the literature a common approach, it entails a high level of uncertainty. Therefore, the trait variables used here can only be viewed as a rough representation of reality instead of a precise metric. From the trait data, we calculated the community-weighted means (CWM) of each trait for each site and census, using the individuals' basal area as weights. Hereafter, the CWM of each trait will be referred to as follows: wood density CWMs as 'WD' and specific leaf area CMWs as 'SLA'.

To represent the dispersion of each functional trait, we calculated their weighted standard deviation per census (referred to as ‘WD dispersion’ and ‘SLA dispersion’). To account for differences in sample size, we applied a randomisation approach with 100 simulations *per* site and averaged the resulting CWMs. In each simulation, we randomly selected 100 tree individuals – the minimum number of trees recorded in a census – from each site to calculate a CWM. For census interval data (i.e., dynamics data) we used the CWMs and dispersions corresponding to the midpoint of the interval, consistent with our approach for other variables.

Phylogenetic diversity

From the total of 942 morphospecies (12 identified to the genus level, 930 to the species level), we standardised all of those identified to the species level with The Plant List, using the package *taxonstand*⁶⁷. Name standardisation aimed to maximize the number of matches between the species recorded in our dataset and the ALLOTB phylogeny, which contains over 350,000 tips⁶⁸. This phylogeny is based on DNA sequences from GenBank and the Open Tree of Life as a backbone (more details in Smith and Brown 2018)⁶⁸. Pruning this large phylogeny to match our dataset resulted in a tree containing ~88% of all species (~94% of the basal area recorded across the censuses). We added to the supplementary information the list of which species were matched from the dataset to the phylogeny (supplementary_data_file_2_species_phytree).

To summarise the evolutionary history of each tree community in each census, we used the R package *picante*⁶⁹ to calculate phylogenetic diversity⁷⁰. Phylogenetic diversity *sensu stricto* is the total sum of branch lengths of all taxa from a community comprised in a phylogeny. Because this metric is highly correlated with species richness⁷¹, we calculated its standardised effect size by comparing each observed value with that obtained under a null expectation. To do this, we randomly shuffled the tips of the phylogeny 999 times and, each time, calculated a phylogenetic diversity value for each randomised phylogeny. The standardised effect size was then computed by subtracting the mean of the randomised values from the observed value and dividing the result by their standard deviation⁶⁹. We used this approach because it enables the detection of high or low evolutionary diversity regardless of species richness, which is sensitive to sampling effort.

Climate data

We extracted multiple temperature, precipitation, and evapotranspiration variables from the Climatic Research Unit (CRU TS version 4.04; released 24 April 2020; <https://crudata.uea.ac.uk/cru/data/hrg>⁷²): mean monthly temperature (°C), mean monthly daily maximum temperature (°C), monthly precipitation (mm) and daily potential evapotranspiration (dPET, mm) with a 0.5° resolution. We used 1-km² resolution temperature and precipitation data from WorldClim⁷³ to downscale the CRU data (except dPET) via the delta spatial downscaling method⁷⁴. From the downscaled data, we calculated the average values of mean annual temperature (MAT), maximum temperature and mean annual precipitation (MAP) across the full years within each census interval. Additionally, we calculated the annual maximum climatic water deficit (CWD) by summing the monthly differences between downscaled precipitation (mP) and potential evapotranspiration (PET), considering only months where PET exceeded mP (i.e., water deficit), following Chave et al. 2014⁷⁵. For the first census of the census-level data (used only in the carbon stocks models), we used the mean climate values from the preceding 5 years. Due to their strong correlation (Figure S8), we used principal component analysis (PCA) to synthesise the climatic variables. The first PCA axis explained 91% of the variance and described a cold-wet to warm-dry climatic gradient (low to high values, respectively). We used this axis in the analyses at both the census and census interval levels. Further details on the PCA are provided in the Statistical Analyses section.

Soil data

In the first census of each site, soil surface samples (20 cm of depth) were collected from three points in each subplot and later combined into one composite sample. Following *Empresa Brasileira de Pesquisa Agropecuária's* protocol⁷⁶, the samples were sent for analysis of the following parameters: pH in water, phosphorus (mg cm⁻³) (P), potassium (mg cm⁻³) (K), calcium (cmolc dm⁻³) (Ca), magnesium (cmol dm⁻³) (Mg), aluminium (cmolc dm⁻³) (Al) and sum of bases (SB) (sum of Ca, K and Mg; cmolc dm⁻³). For each site, we used the mean value of each soil variable measured across its subplots. Due to strong correlation among the soil variables, we also used PCA to synthesise edaphic variation. The first three PCA axes, which explained 89% of the variance (63.8 %, 12.7 % and 12%, respectively), were retained for analysis. The first axis was positively associated with soil fertility – characterized by higher levels of pH, P, K, Ca, Mg and SB, and lower levels of Al. The second axis was positively

associated with Al and P, while the third was positively associated with Mg and negatively with P. More details on the PCA are provided in the Statistical Analyses section.

Controlling for edge effects

Edge effects on forest microclimatic conditions can affect carbon dynamics through changes in plant community composition, phenology, forest structure, and plant growth^{77,78}. Since our sampling design aimed to maximise the area covered within each site, smaller sites tended to have greater exposure to edge effects. Hence, to control for the influence of edge effects in carbon dynamics, we included site area in the models. More details are provided in the Statistical Analyses section.

Statistical analysis

We performed all statistical analyses in the R environment version 4.0.2⁷⁹, using the following packages for graphics: *ggplot2*, *GGally*, *grDevices*, *cowplot*, *viridis* and *corrplot*^{80,81,82,83,79,84}. To account for the non-independence of repeated observations within sites over time (e.g., multiple censuses and intervals per site), we included random intercepts for site in all models. This approach accounts for temporal autocorrelation and site-level variation by allowing each site to have its own baseline, thus controlling for within-site dependence inherent to long-term forest monitoring.

We used linear mixed-effects models (LMM) from the package *lme4*⁸⁵ and generalised additive models (GAM) from *mgcv*⁸⁶. Due to different spatial and temporal sampling efforts across sites, we weighted the observations by area sampled and census interval length (Figure S1). For the forest and carbon dynamics models, we used the following weighting procedure, following Hubau et al. 2020¹: $\text{interval length}^{1/3} + \text{sampled area}^{1/4} - 1$. The carbon stocks models were weighted by the cubic root of the sampled area¹⁴, while the temporal climatic trend models were weighted by the cubic root of interval length. To meet model assumptions (normality and homoscedasticity of residuals), avoid negative predictions, and handle extreme values (e.g., site area), we constrained all predictors to positive values and applied a log-transformation. To facilitate comparisons among effect sizes, the predictors were centred to zero-mean and scaled to unit variance, allowing effect sizes to be interpreted as the change in the response variable associated with a one-standard-deviation increase in the predictor. Using the package *spdep*⁸⁷, we tested for spatial autocorrelation in model residuals with Moran's I. The results indicated

no significant spatial autocorrelation, suggesting that spatial dependencies among observations did not bias model inferences.

Long-term carbon, vegetation, and climate trends were regressed as a function of time (year) using GAMs (Equation 1). To maximise the use of available data, we used census-level instead of interval-level data – particularly for carbon stocks (also for LMMs models), taxonomic diversity, phylogenetic diversity, and trait variables. Since no model selection would be performed, we used Restricted Maximum Likelihood (REML) for the GAM model fits. We did not use GAMs in further analyses due to the relatively small sample size, which would not support the estimation of numerous parameters. In models with multiple predictors and interactions, detailed below, the large number of smooth splines would risk overfitting.

Other than the long-term carbon trends, we also fitted GAMs to evaluate the relationships between the carbon variables and other predictors (Equation 2). Hence, carbon stocks and carbon dynamics (in absolute and relative values) were modelled as a function of site area (i.e., proxy for edge effects), soil and interactions between time (year) and multiple ecological variables (i.e., taxonomic diversity, phylogenetic diversity, WD dispersion, SLA dispersion, WD CWM, and SLA CWM).

As previously mentioned, climate and soil data were synthesised by principal component analysis (PCA). For each set of variables (either climate or soil), we centred and scaled all original variables and then submitted them to a PCA using the R packages *FactoMineR*⁸⁸ and *factoextra*⁸⁹. Climate was described by its first PCA axis, while soil was described by its first three PCA axes.

We tested the inclusion of spatial cluster as a predictor in the models. However, the strong association between cluster and climate due to the broad latitudinal gradient captured by the clusters resulted in extremely high VIF in models where cluster and climate were both included as predictors. Hence, we opted for the inclusion of climate instead of spatial cluster for two main reasons: first, for being a tangible, continuous variable instead of an arbitrary, discrete variable; second, for capturing within-cluster climate variation.

We allowed year to interact with climate and the ecological variables (Equation 2). The climate-year interaction was added due to strong interactive effects reported in a previous study², which used a large portion of the data used here. For these analyses, the LMM were fitted using Maximum Likelihood because model selection, detailed below, can be biased by REML.

$$\text{Carbon} \sim \text{Year} + (1 | \text{Site})$$

Vegetation
Climate

Equation 1

Carbon stocks
Carbon dynamics
Carbon dynamics (%)

$\sim \text{Site area} + \text{Soil} + (\text{Climate} + T.\text{diversity} + P.\text{diversity} + \text{Trait dispersion} + \text{Trait CWM}) * \text{Year} + (1 | \text{Site})$

Equation 2

In the equations above, “*” is an interaction term, which includes the main effects of each separate variable and their interaction effects, “+” is the additive effects (i.e., main effects) and “(1 | site)” refers to the random intercepts of sites.

Model selection was based on the Akaike Information Criterion of second order (AICc). We followed a three-step procedure. First, starting from a global model including all explanatory variables, we fitted submodels with all possible combinations of the following predictors: *year*, *site area*, *climate*, and *soil* (Equation 2). Second, we ranked the submodels by their AICc values. Third, through multimodel inference, we averaged the coefficients of the best-performing submodels ($\Delta\text{AICc} \leq 4$) and used their conditional averages in the final model⁹⁰. To avoid multicollinearity (Figures S9-S24), we only retained predictors with a variance inflation factor ($\text{VIF} \leq 5$), except for those involved in interaction terms, where a $\text{VIF} < 10.5$ was tolerated. This exception was necessary because interaction terms inherently increase VIF values due to variable repetition. In our models, this applied only to climate, which remained a strong predictor despite a high VIF. Although AICc penalises model complexity to reduce overfitting, we further constrained model complexity by requiring at least 10 observations per predictor.

We did not calculate the relative importance of predictors because Akaike weights are biased when predictors are not included in the same number of models, as was our case. For each final model ($\Delta\text{AICc} = 0$), we report the variance explained by the fixed effects (R^2). Model selection, multimodel inference, and R^2 calculations were performed using the *MuMIn* package⁹¹. All effects sizes, P-values and 95% confidence intervals are reported in the main text, figures, or supplementary information.

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Authors contribution

V.A.M., C.R.d.S, J.D.M, J.A.P.J, N.d.A.-C, R.M.d.S, A.C.S, P.H, M.A.L.F, C.L.F., F.M.G., N.C.A.F, G.G.P.d.P, A.B.M.S, W.B.d.S, F.d.C.A, F.d.O., L.C.A.d.S, R.T.P., (A.M.d.S.S, L.A.S.F, M.G.R, D.M.M, V.F.P.d.L.e.S, A.L.d.C.R, R.d.S.M, M.d.O.A.B) collected and/or processed the data. C.L.F., R.M.d.S, J.A.P.J, A.C.S, P.H. curated the data. V.A.M., T.M.C.-S., N.d.A.-C analysed the data. V.A.M. performed the statistical analyses. V.A.M., C.R.d.S, J.D.M, F.C.d.S., J.A.P.J, N.d.A.-C, A.C.S, P.H and R.M.d.S. conceived the ideas and designed methodology. V.A.M., N.d.A.-C and F.C.d.S. led the writing of the manuscript. J.A.P.J, J.D.M. edited the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Competing interests

There are no competing interests.

Data Availability

Raw data from the forest inventories are hosted in the ForestPlots.net system and bound to data-use restrictions defined on Forestplots.net (www.forestplots.net) (see area codes in data file S1). All data needed to evaluate the conclusions in the paper are present in the Supplementary Materials (data files: census_level.csv and census_int_level.csv). The codes will be available at publication (during revision they can be accessed upon request).

Code Availability

The codes can be found here:

https://drive.google.com/drive/folders/157Ge4kh18LN8JEN_bjScmdEfjdX1VhEq?usp=sharing

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Supplementary figures

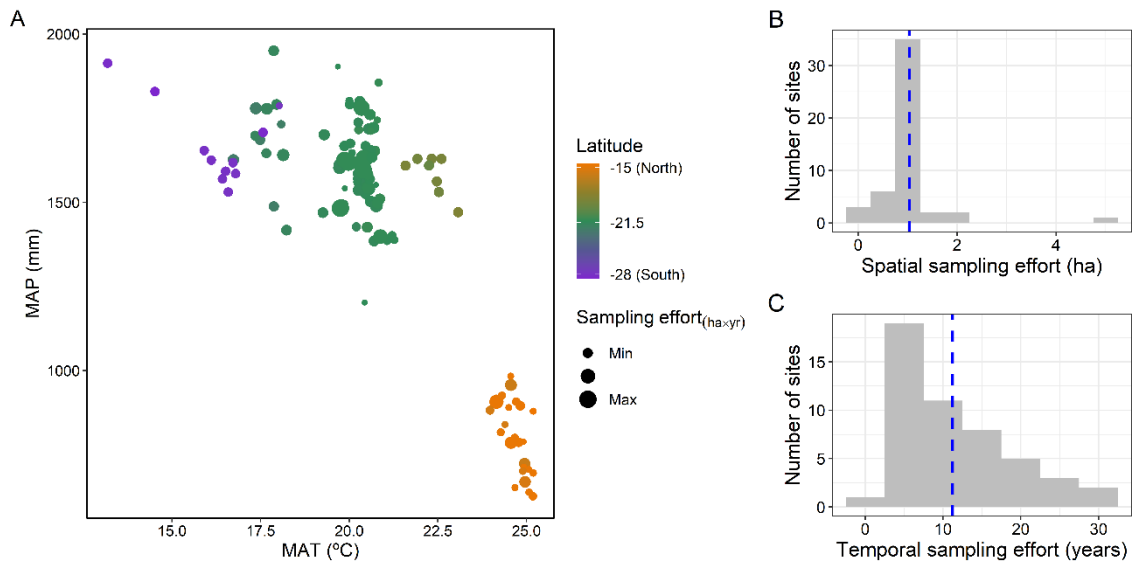


Figure S1. Distribution of the sampled sites across the climate space and their spatial and temporal sampling efforts. A) Distribution of the sites along the climate space represented by mean annual temperature (MAT) and mean annual precipitation (MAP). The points are census intervals ($n = 114$), and their sizes are proportional to the site sampled area (mean 1.03 ha) times interval length (mean 5 years). B) Frequency of site sampled areas ($n = 49$). The blue dashed line is the mean of the sampled area among sites (1.03 ha). C) Frequency of site total monitoring length ($n = 49$) (year of the last census minus year of the first census). The blue dashed line is the mean of the total monitoring length among sites (11 years).

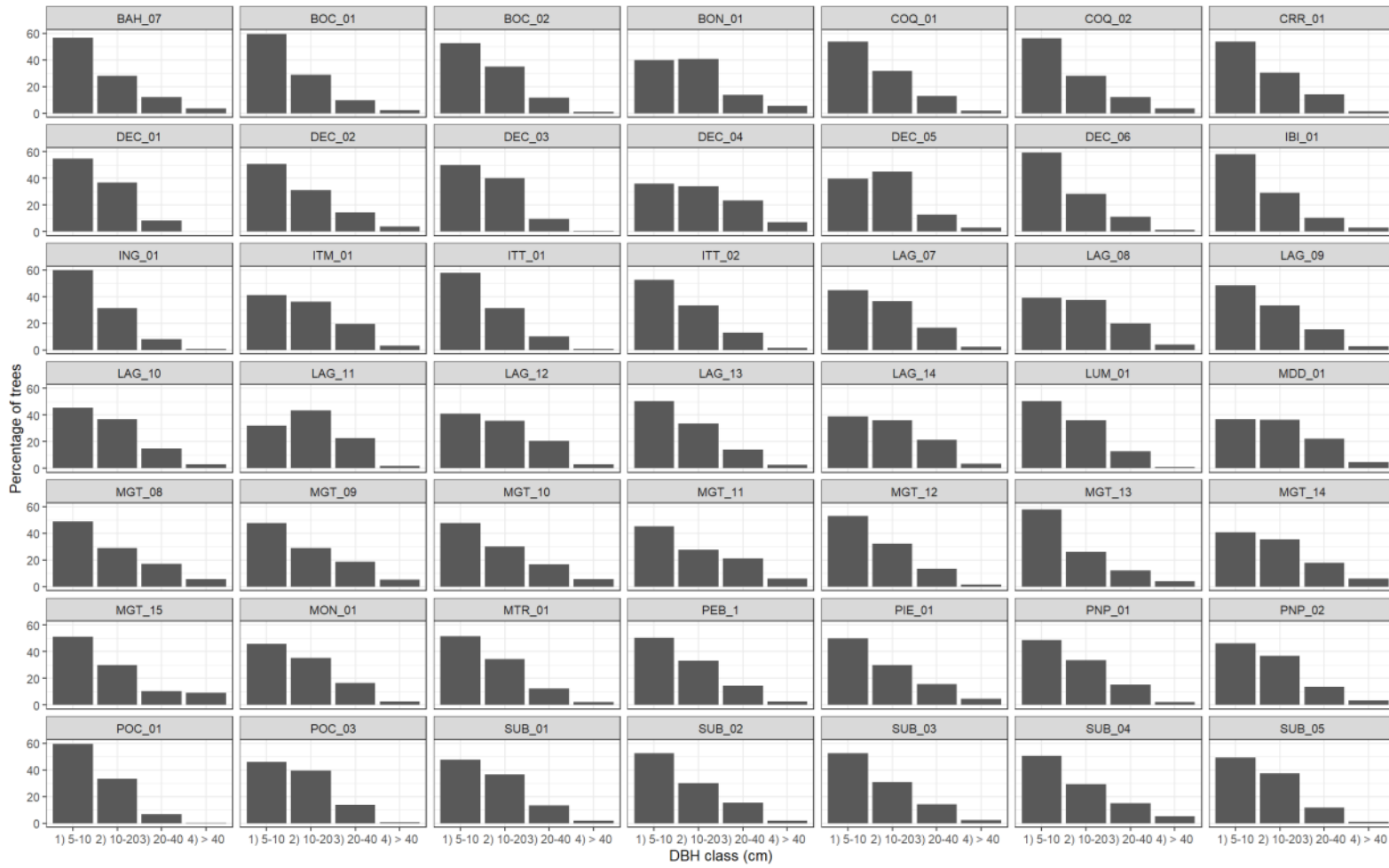


Figure S2. Diametric distribution of tree individuals by site. The y axis is the percentage of trees relative to the total number of trees in the site.

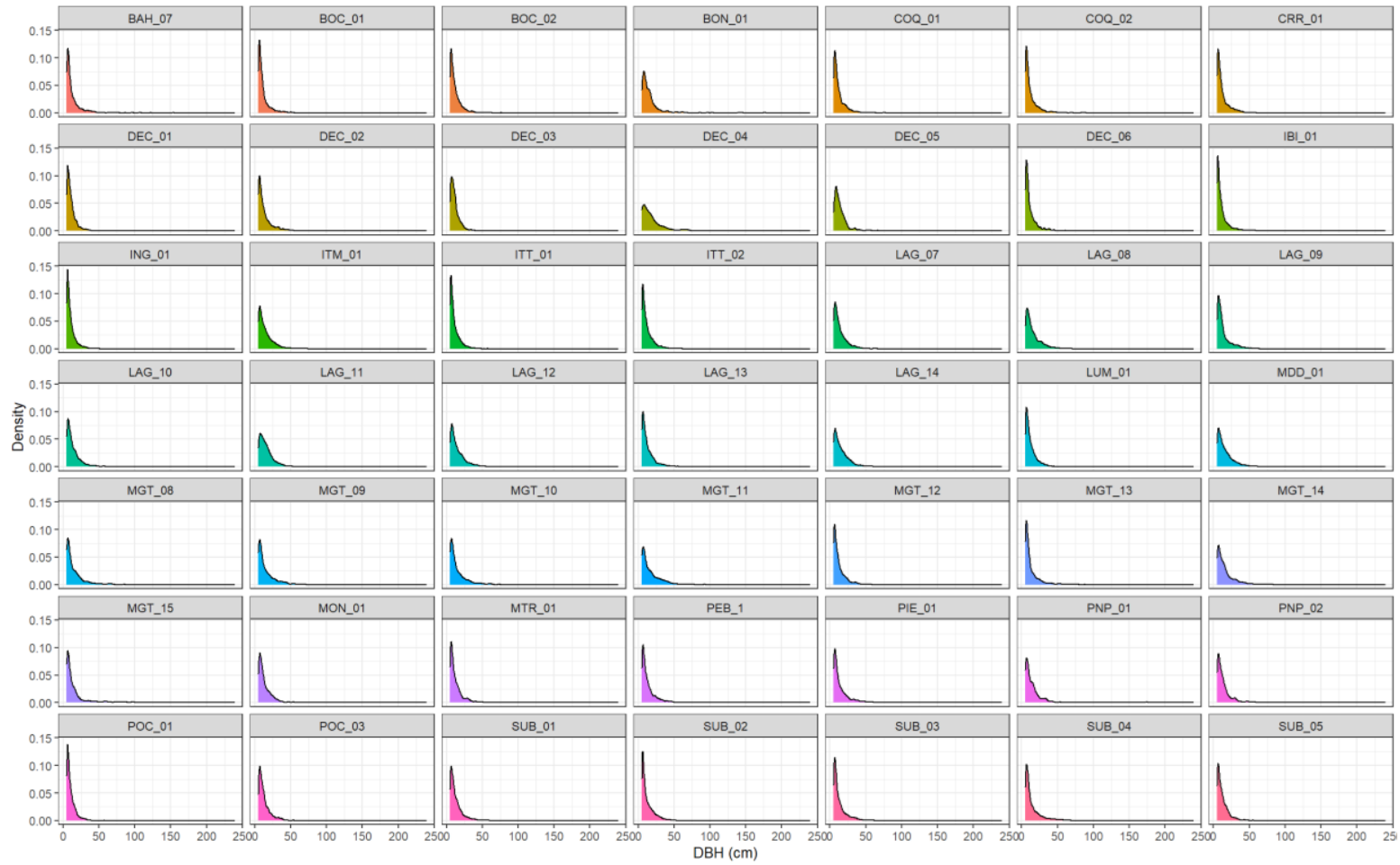


Figure S3. Density of tree individuals by DBH for each site.

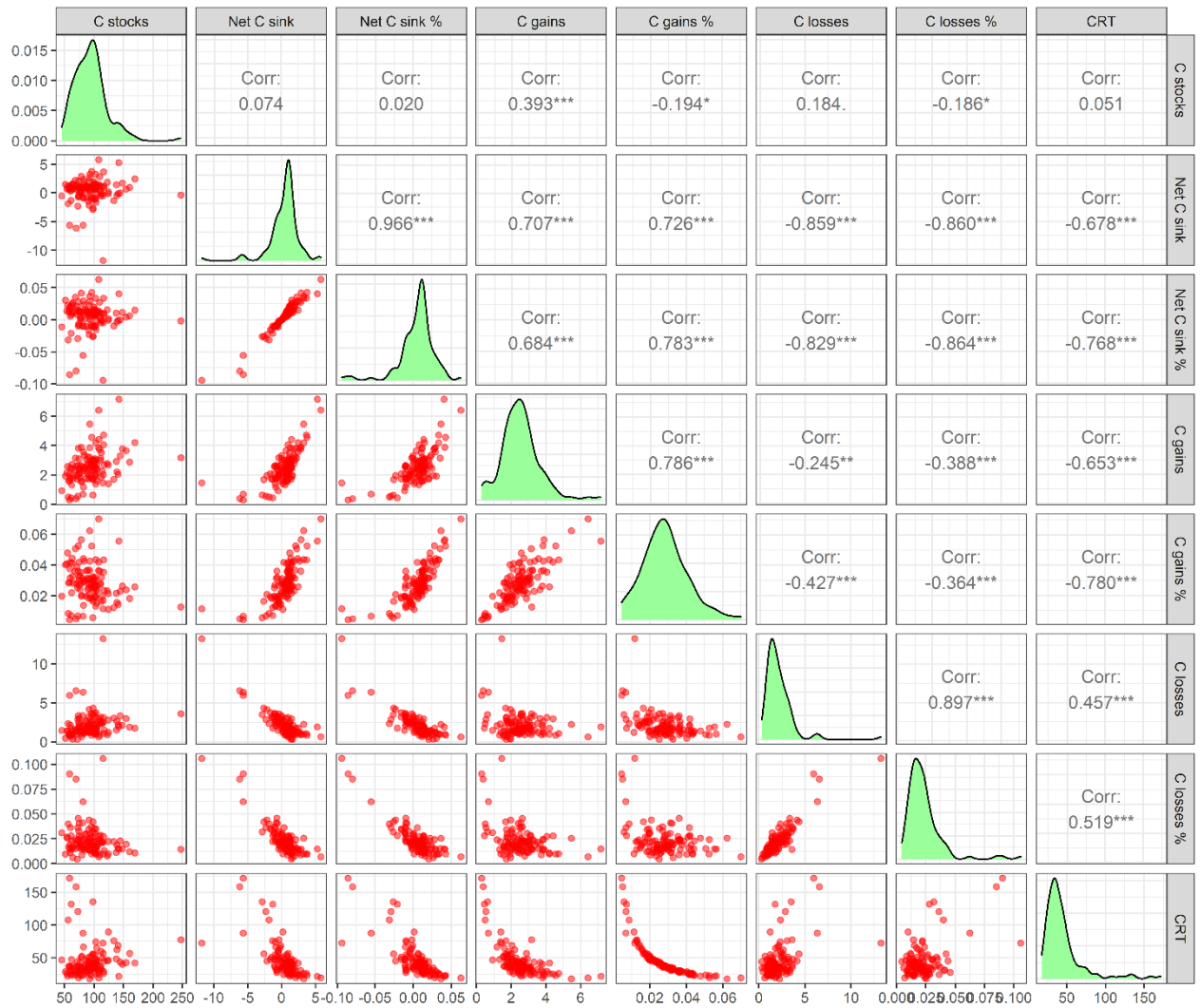


Figure S4. Correlation, scatter plots and density of each carbon dynamics variable. Variables followed by % are the values relativized by carbon stocks.

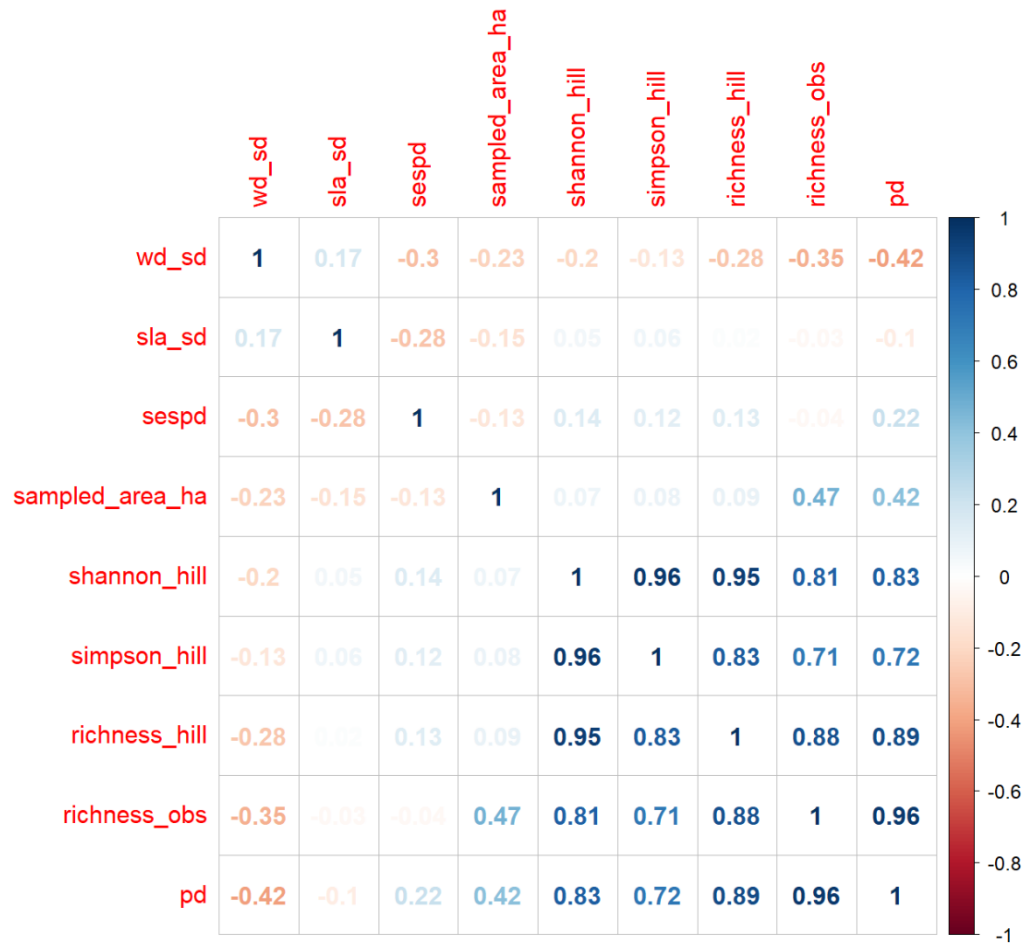


Figure S5. Correlation between ecological variables (including sampled area). Wood density dispersion (wd_sd), specific leaf area dispersion (sla_sd), phylogenetic diversity (standardized value; sespd), sampled area in hectares (sampled_area_ha), Shannon diversity Hill number (Shannon_hill), species richness Hill number (richness_hill), observed species richness (richness_obs) and phylogenetic diversity (PD; pd).

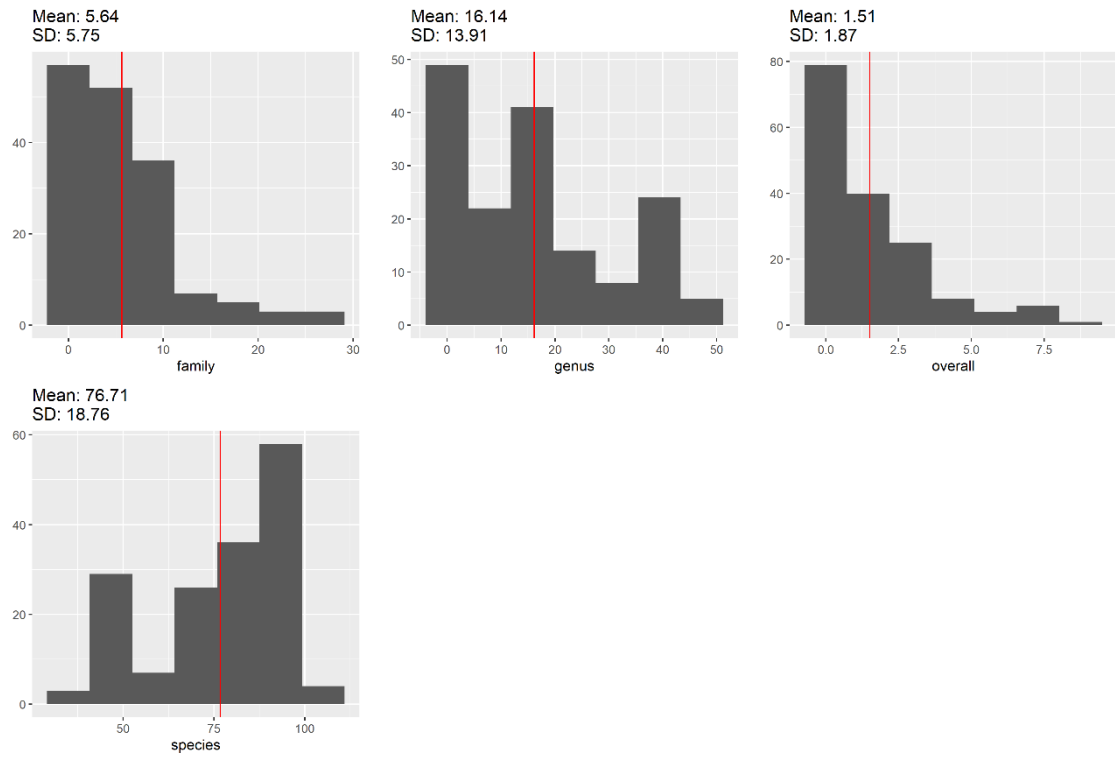


Figure S6. Distribution of the representativity (relative carbon stocks) of species-level trait information among census of specific leaf area (SLA).

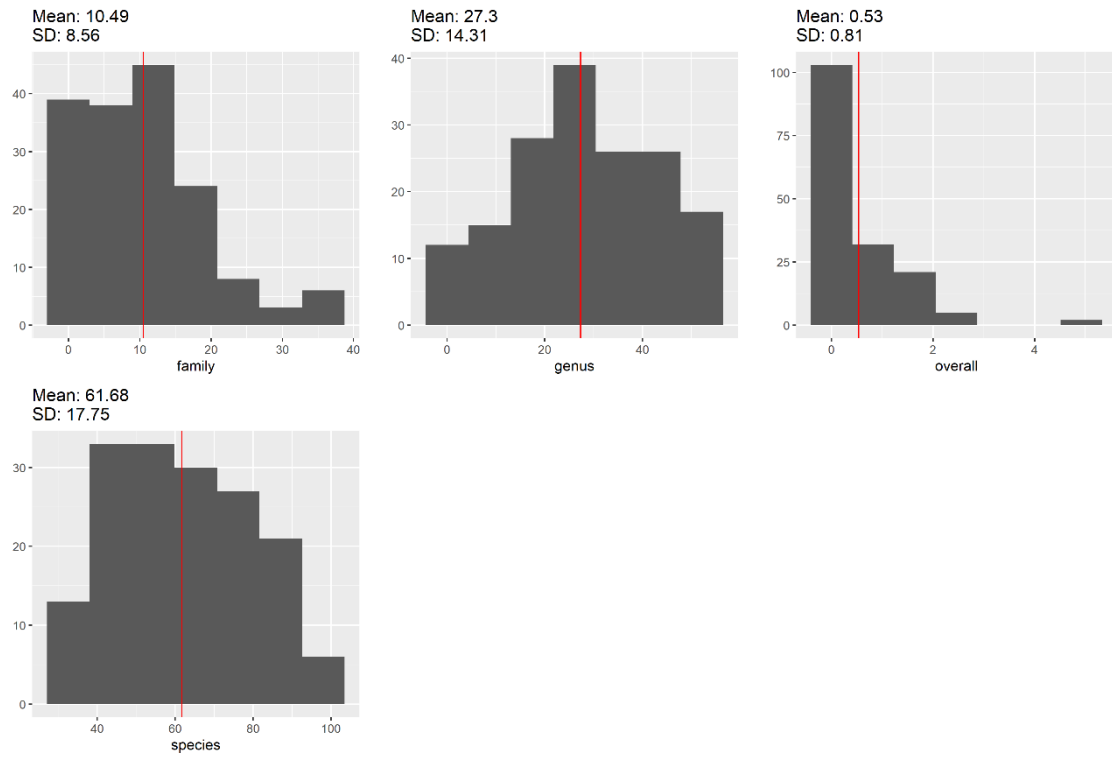


Figure S7. Distribution of the representativity (relative carbon stocks) of species-level trait information among census of wood density (WD).

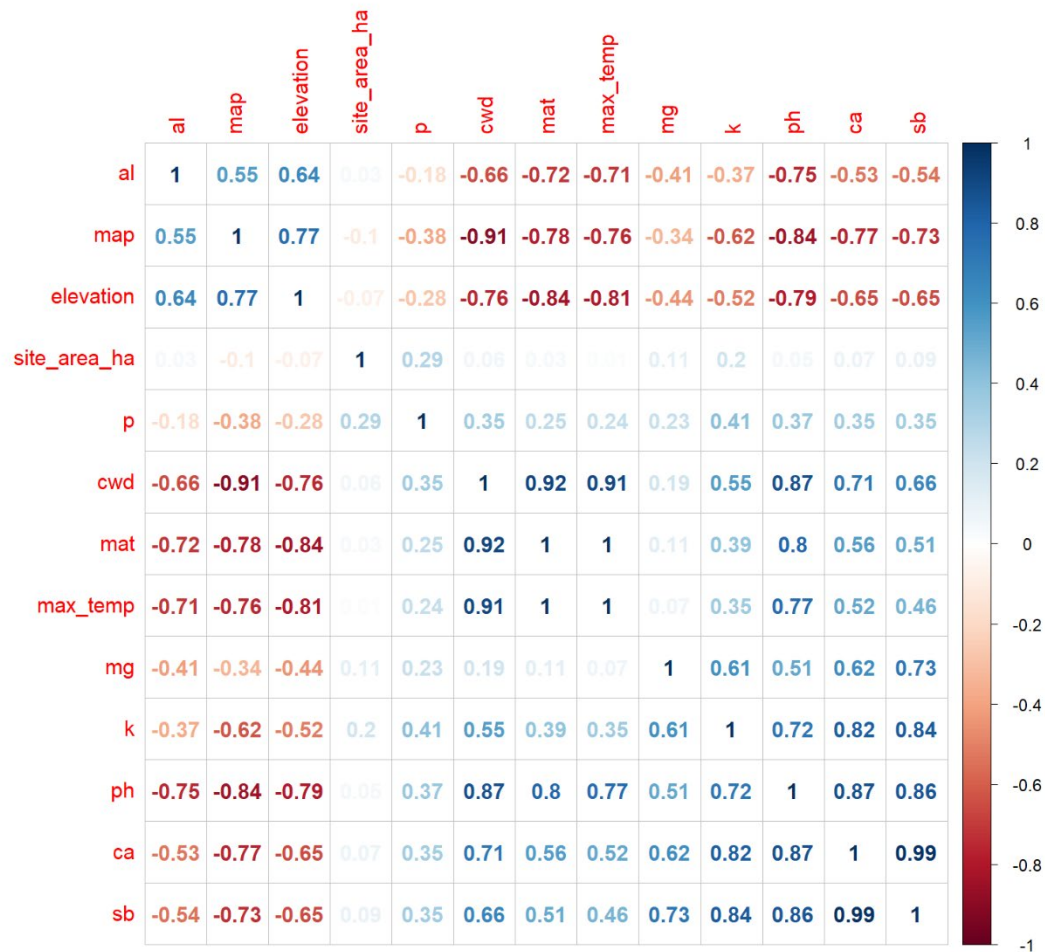


Figure S8. Correlation between environmental variables (climate and soil), altitude (elevation) and site area in hectares (site_area_ha). Mean Annual Temperature (mat), Maximum Temperature (max_temp), Mean Annual Precipitation (map), and Climatic Water Deficit (cwd), pH (ph), Phosphorus (p), Potassium (k), Calcium (ca), Magnesium (mg), Aluminum (al), and Base Saturation (sb).

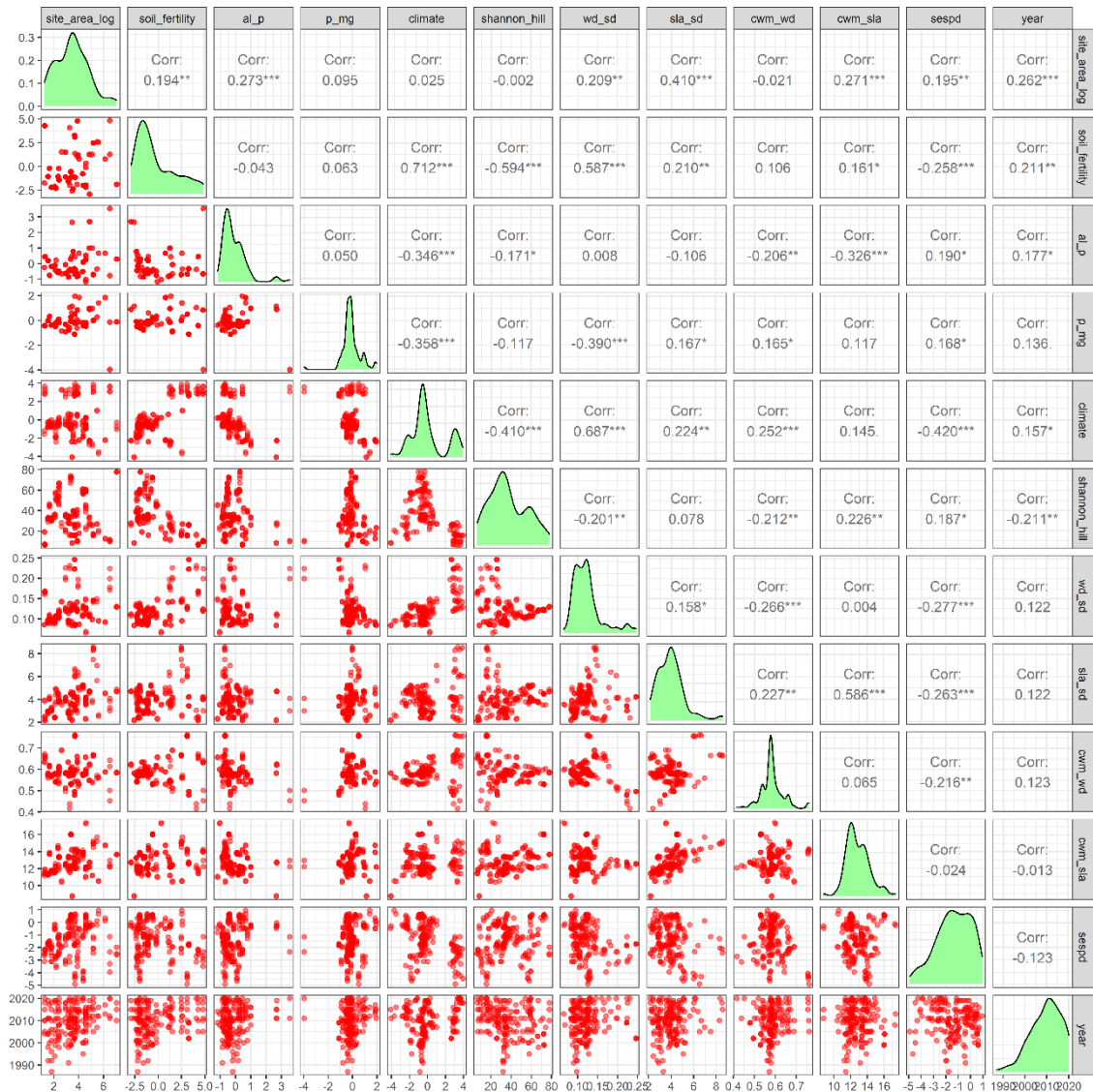


Figure S9. Correlation, scatter plots and density of the predictors of the carbon stocks model ($n = 163$). Site area in hectares in log scale (site_area_log), soil fertility PCA axis (soil_fertility), aluminim-phosphors PCA axis (al_p), phosphorus -> magnesium PCA axis (p_mg), cold-wet > warm-dry PCA axis (climate), taxonomic diversity (shannon_hill), WD dispersion (wd_sd), SLA dispersion (sla_sd), community weighted mean of WD (wd_cwm), community weighted mean of SLA (sla_cwm), phylogenetic diversity (sespd) and year (year).

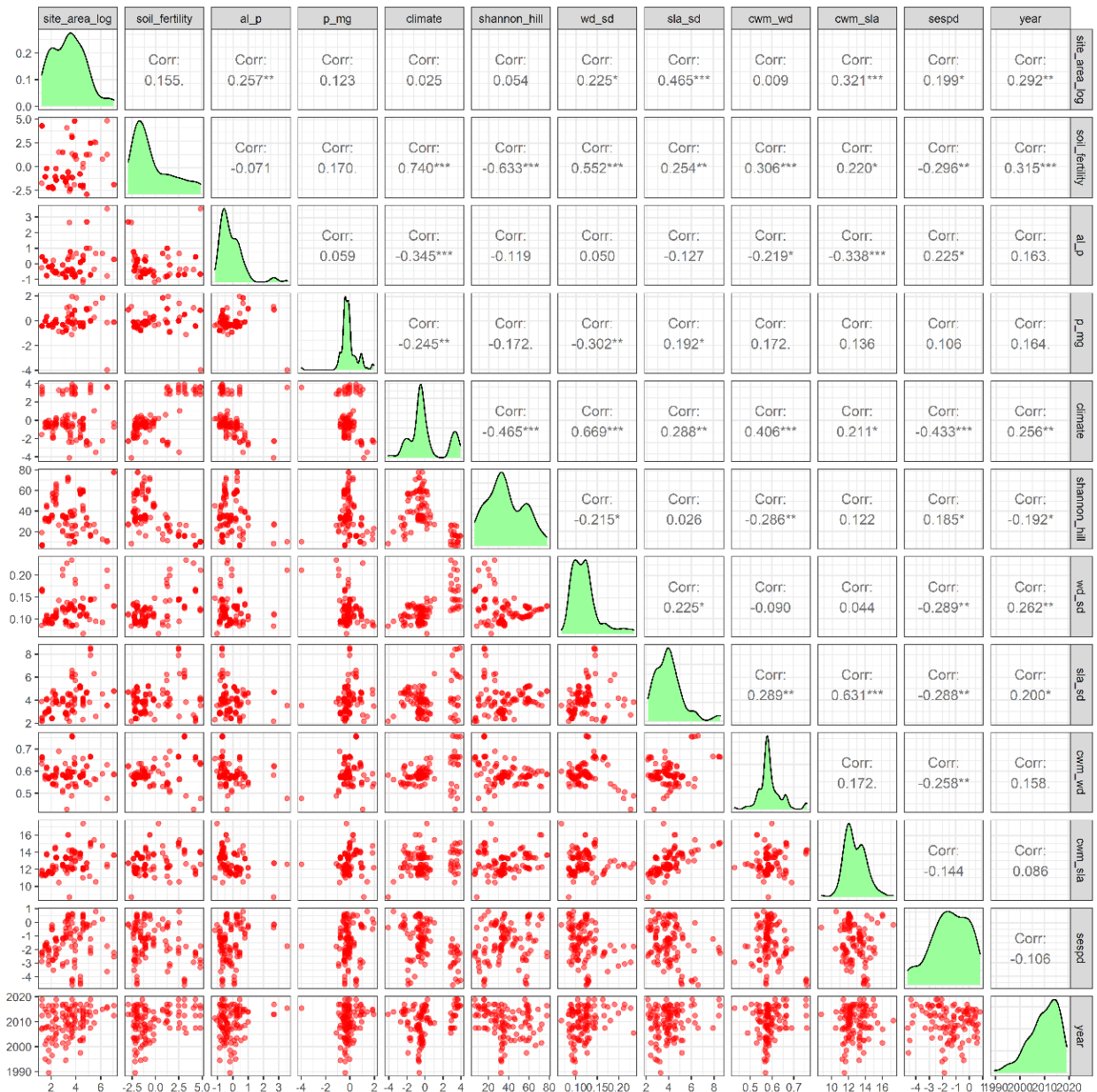


Figure S10. Correlation, scatter plots and density of the predictors of the carbon dynamics models ($n = 114$). Site area in hectares in log scale (site_area_log), soil fertility PCA axis (soil_fertility), aluminim-phosphors PCA axis (al_p), phosphorus -> magnesium PCA axis (p_mg), cold-wet -> warm-dry PCA axis (climate), taxonomic diversity (shannon_hill), WD dispersion (wd_sd), SLA dispersion (sla_sd), community weighted mean of WD (wd_cwm), community weighted mean of SLA (sla_cwm), phylogenetic diversity (sespd) and year (year).

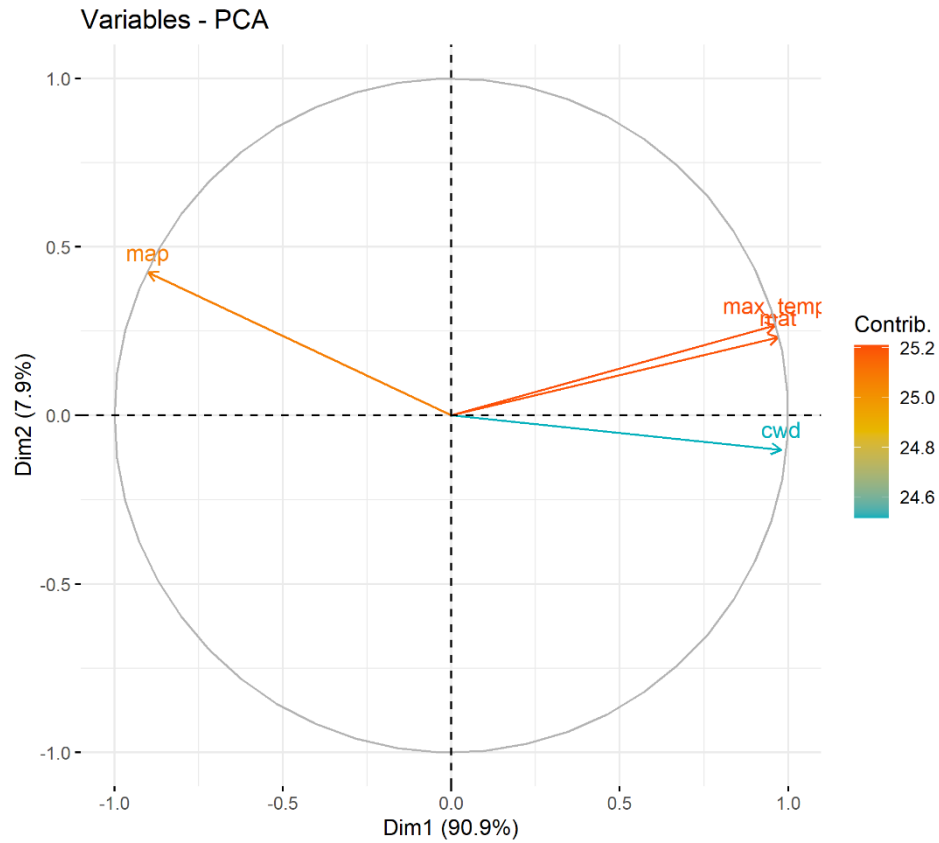


Figure S11. Principal Component Analysis (PCA) Biplot of Climate Variables at census level. This PCA biplot visualizes the relationship among four climate variables: Mean Annual Temperature (mat), Maximum Temperature (max_temp), Mean Annual Precipitation (map), and Climatic Water Deficit (cwd). The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

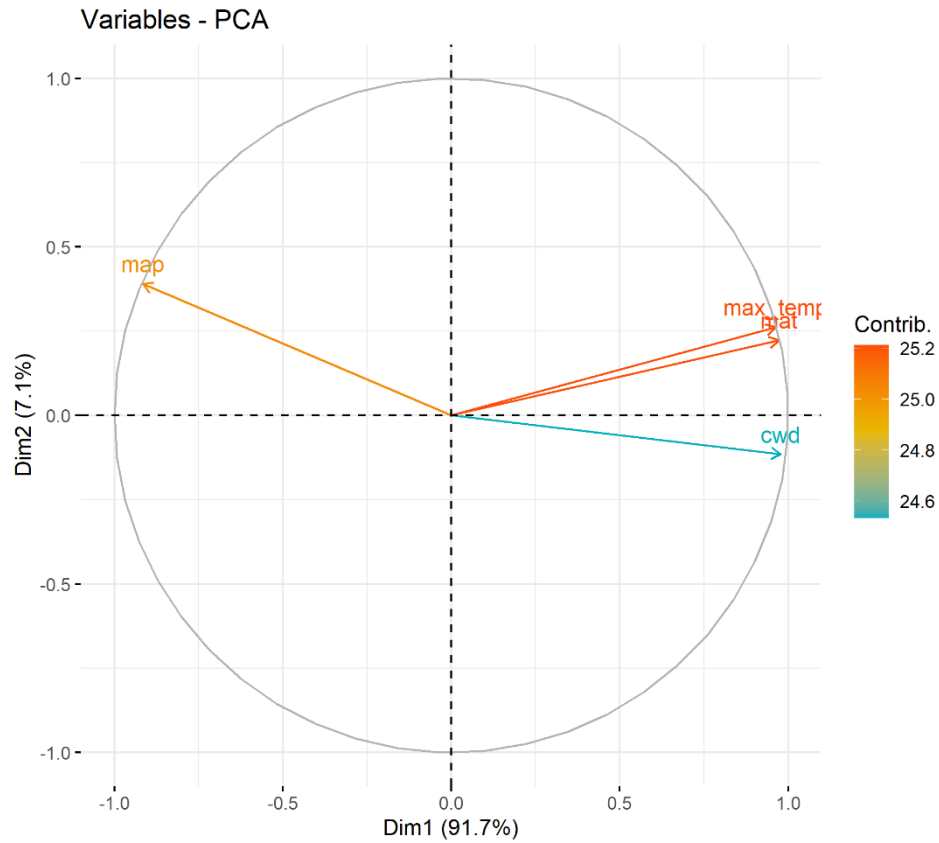


Figure S12. Principal Component Analysis (PCA) Biplot of Climate Variables at census interval level. This PCA biplot visualizes the relationship among four climate variables: Mean Annual Temperature (mat), Maximum Temperature (max_temp), Mean Annual Precipitation (map), and Climatic Water Deficit (cwd). The analysis encompasses data aggregated over complete years within each interval ($n = 114$).

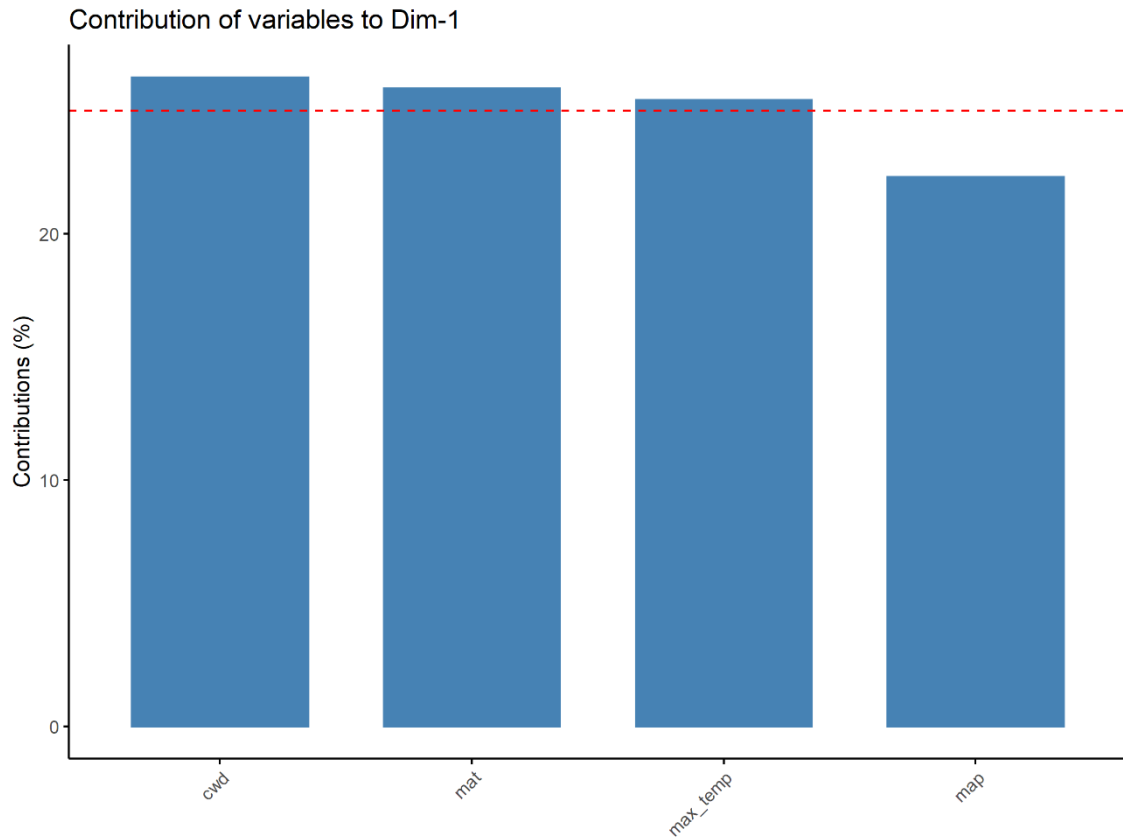


Figure S13. Contribution Plot of Climate Variables at Census Level. This contribution plot displays the contribution of four climate variables—Mean Annual Temperature (mat), Maximum Temperature (max_temp), Mean Annual Precipitation (map), and Climatic Water Deficit (cwd)—to the first principal component (PC1) on the y-axis. The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

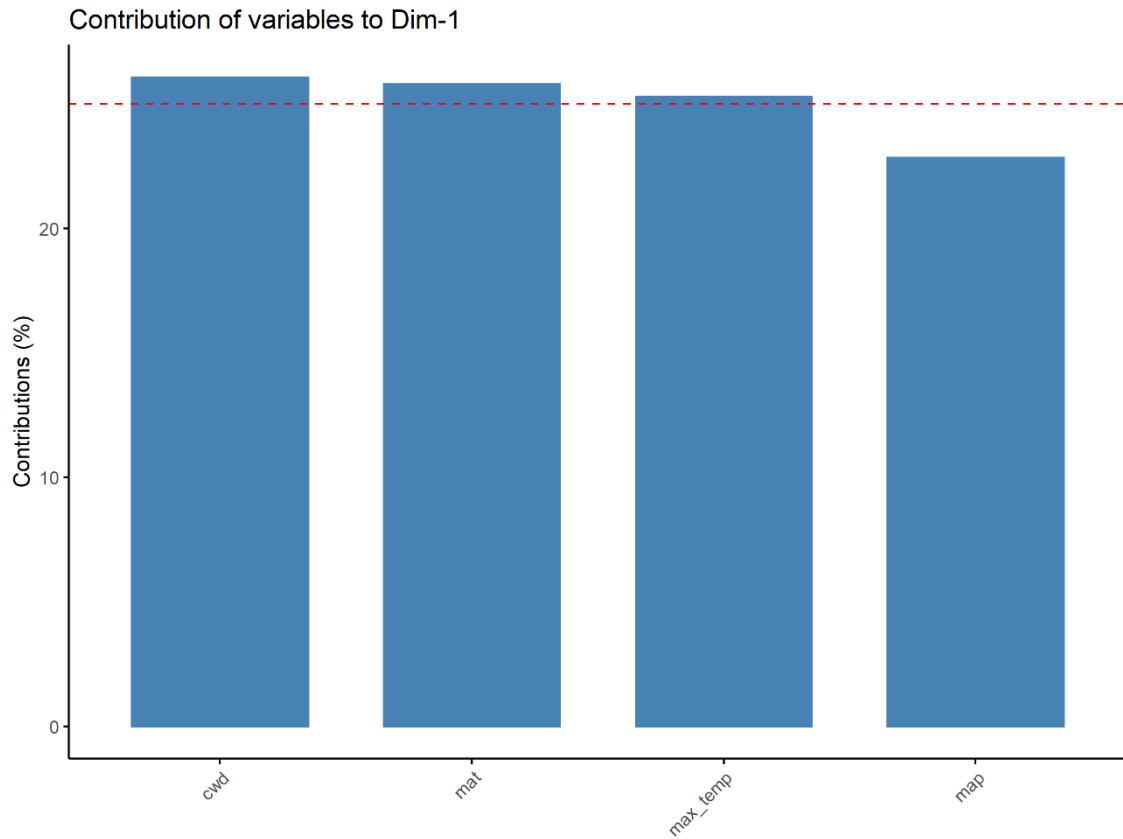


Figure S14. Contribution Plot of Climate Variables at Census Interval Level. This contribution plot displays the contribution of four climate variables—Mean Annual Temperature (mat), Maximum Temperature (max_temp), Mean Annual Precipitation (map), and Climatic Water Deficit (cwd)—to the first principal component (PC1) on the y-axis. The analysis encompasses data aggregated over complete years within each interval ($n = 114$).

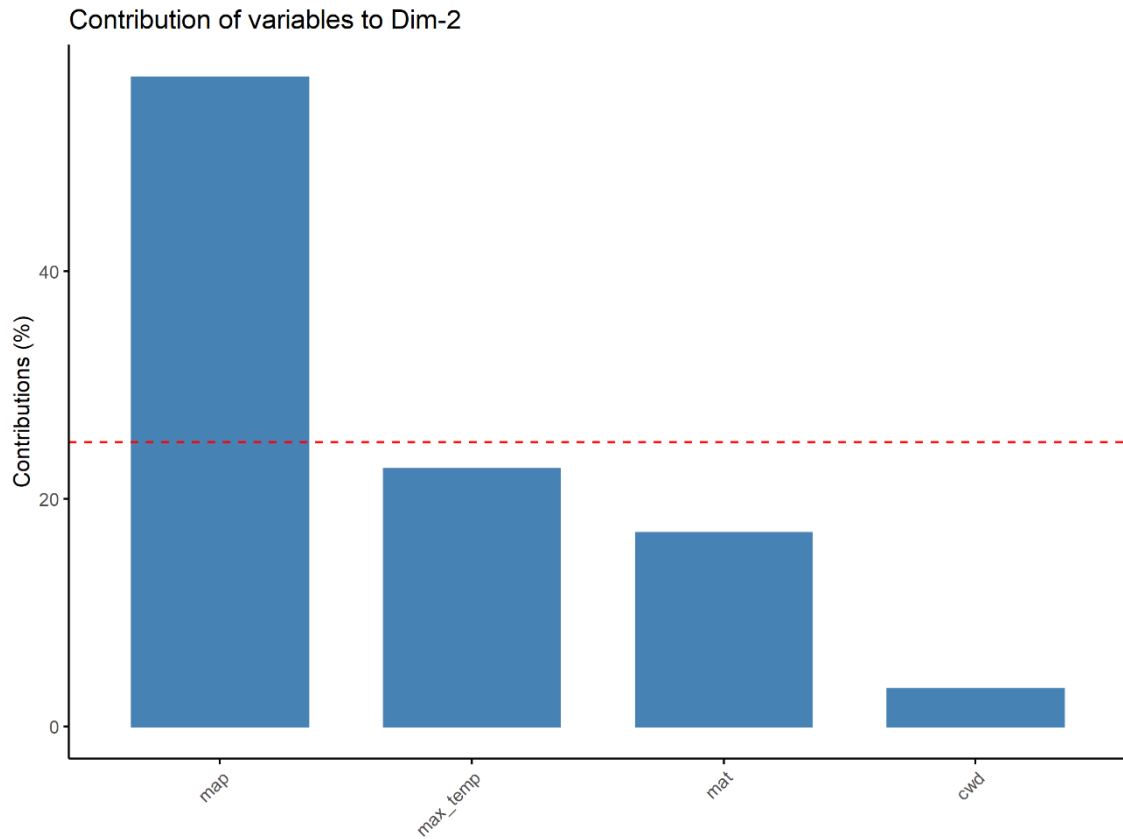


Figure S15. Contribution Plot of Climate Variables to PC2 at Census Level. This contribution plot displays the contribution of four climate variables—Mean Annual Temperature (mat), Maximum Temperature (max_temp), Mean Annual Precipitation (map), and Climatic Water Deficit (cwd)—to the second principal component (PC2) on the y-axis. The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

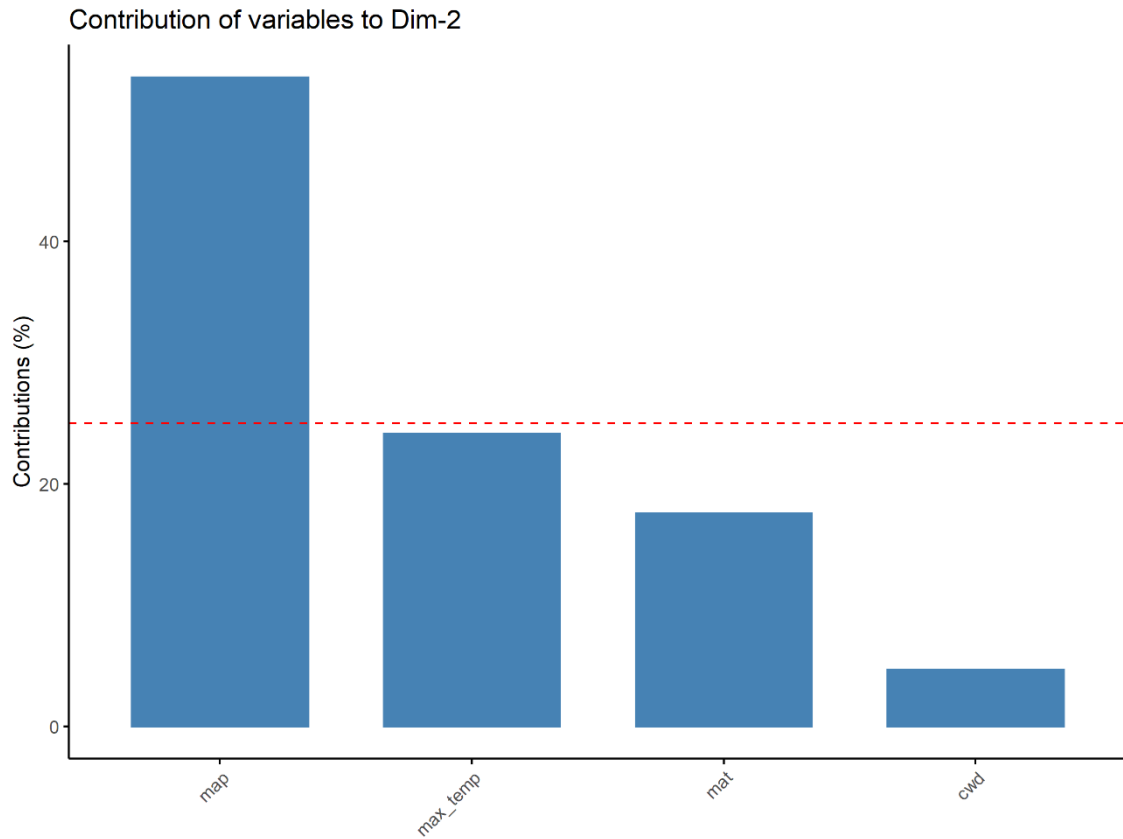


Figure S16. Contribution Plot of Climate Variables to PC2 at Census Interval Level. This contribution plot displays the contribution of four climate variables—Mean Annual Temperature (mat), Maximum Temperature (max_temp), Mean Annual Precipitation (map), and Climatic Water Deficit (cwd)—to the second principal component (PC2) on the y-axis. The analysis encompasses data aggregated over complete years within each interval ($n = 114$).

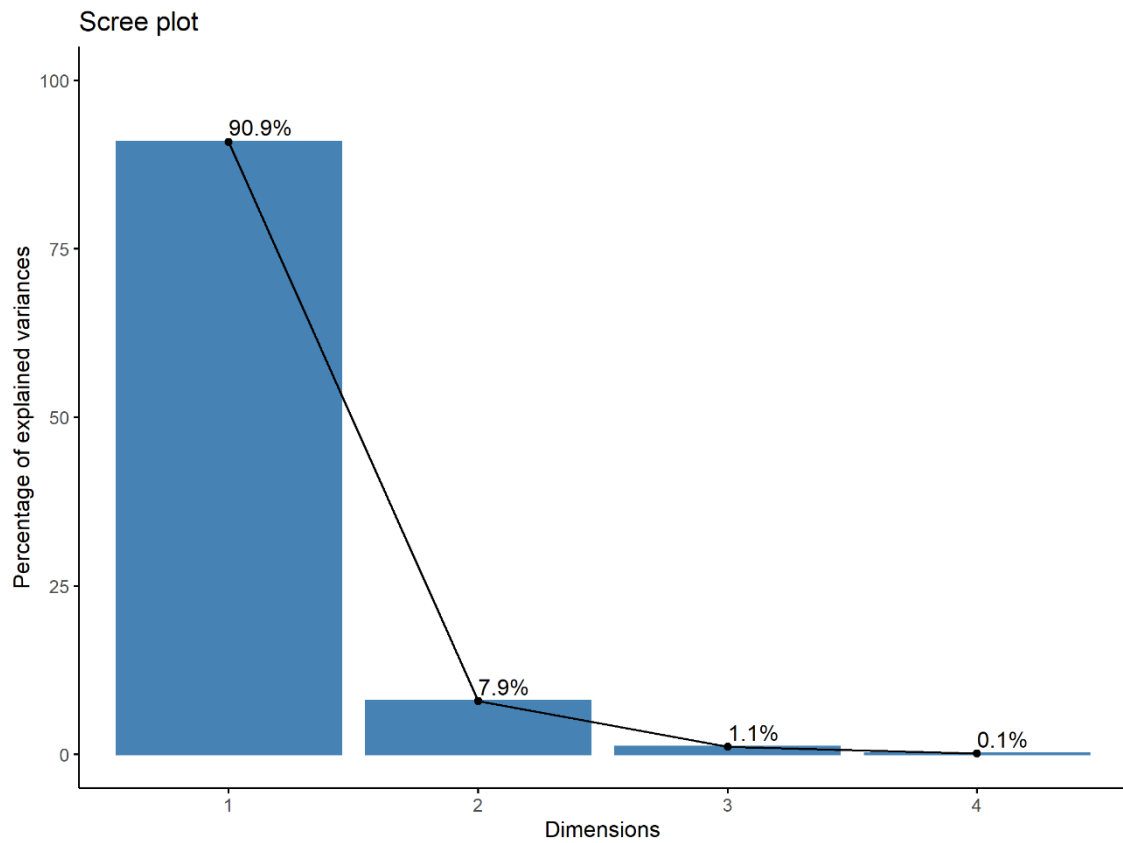


Figure S17. Scree Plot of Principal Components at Census Level. This scree plot shows the percentage of explained variance of the principal components derived from climate data at the census level. The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

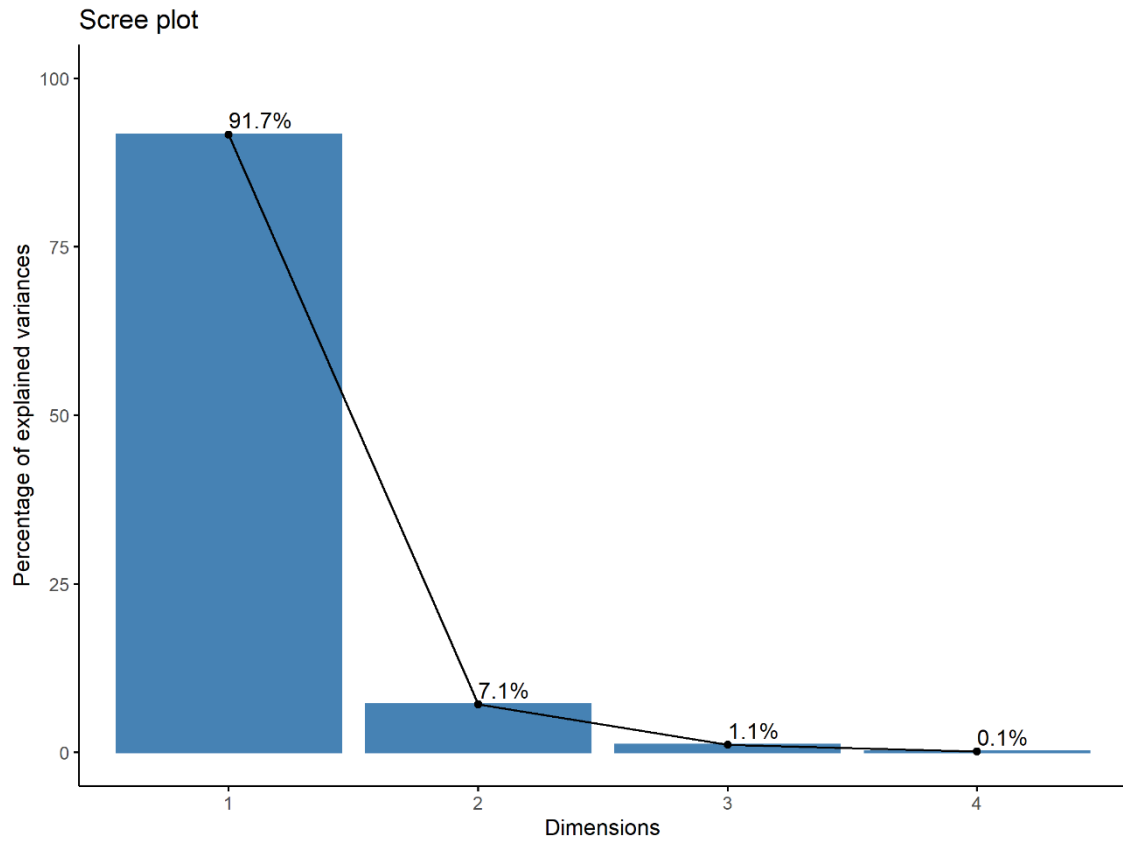


Figure S18. Scree Plot of Principal Components at Census Interval Level. This scree plot shows the percentage of explained variance of the principal components derived from climate data at the census interval level. The analysis encompasses data aggregated over complete years within each interval ($n = 114$).

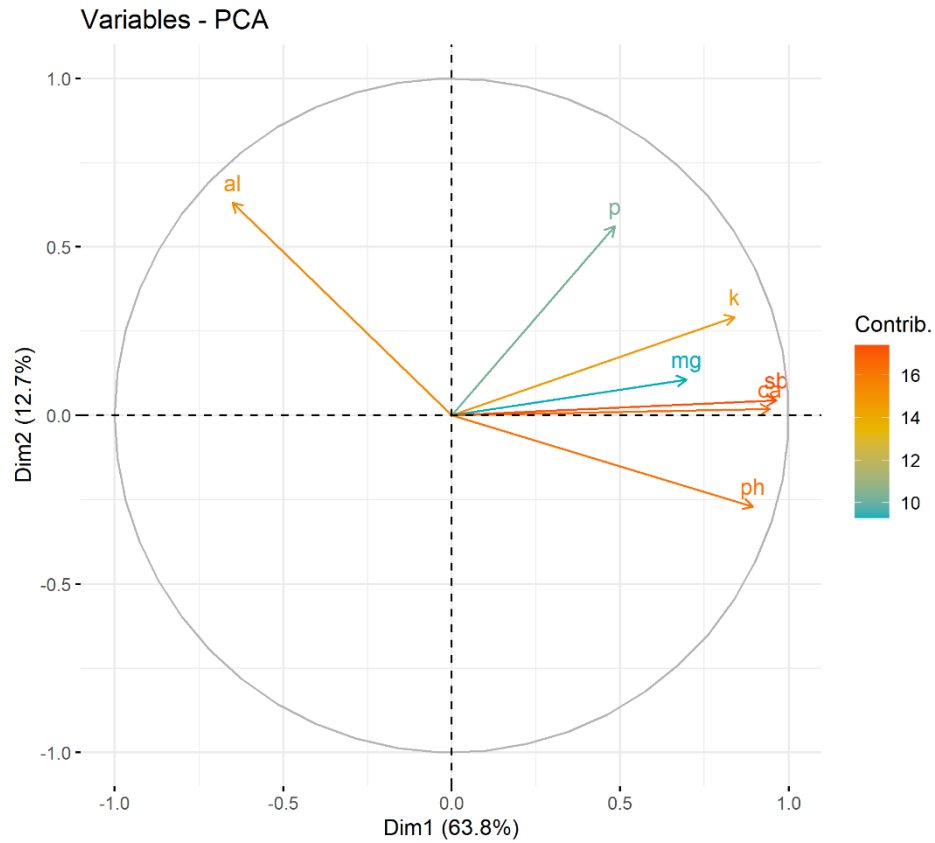


Figure S19. Principal Component Analysis (PCA) Biplot of Soil Variables (Dim1 vs Dim2) at Census Level. This PCA biplot visualizes the relationship among seven soil variables: pH (ph), Phosphorus (p), Potassium (k), Calcium (ca), Magnesium (mg), Aluminum (al), and Base Saturation (sb). The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

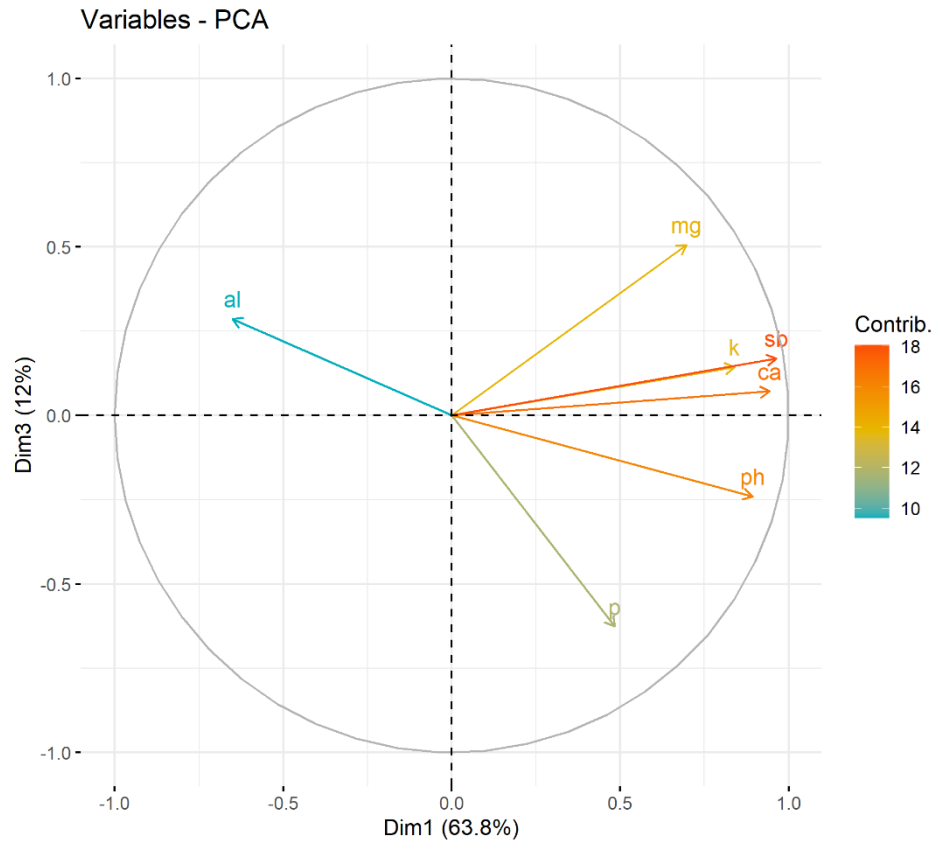


Figure S20. Principal Component Analysis (PCA) Biplot of Soil Variables (Dim1 vs Dim3) at Census Level. This PCA biplot visualizes the relationship among seven soil variables: pH (ph), Phosphorus (p), Potassium (k), Calcium (ca), Magnesium (mg), Aluminum (al), and Base Saturation (sb). The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

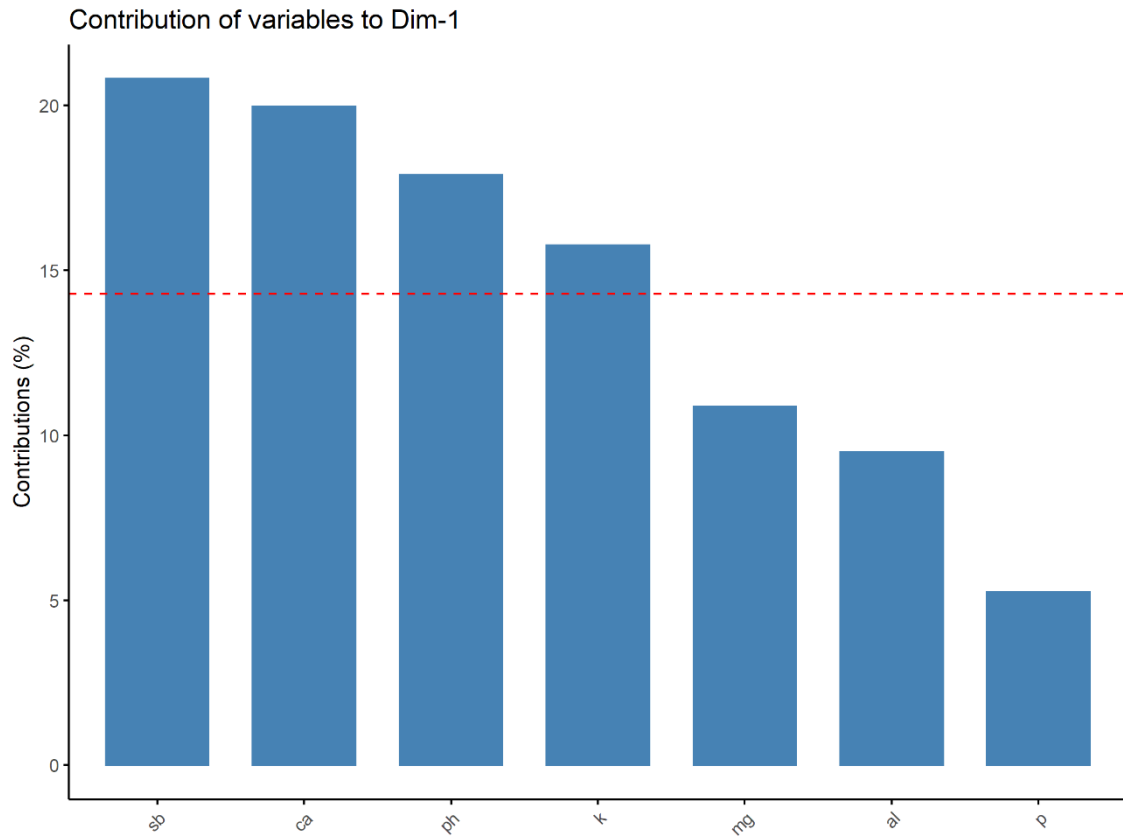


Figure S21. Contribution Plot of Soil Variables to PC1 at Census Level. This contribution plot displays the contribution of seven soil variables—pH (ph), Phosphorus (p), Potassium (k), Calcium (ca), Magnesium (mg), Aluminum (al), and Base Saturation (sb)—to the first principal component (PC1) on the y-axis. The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

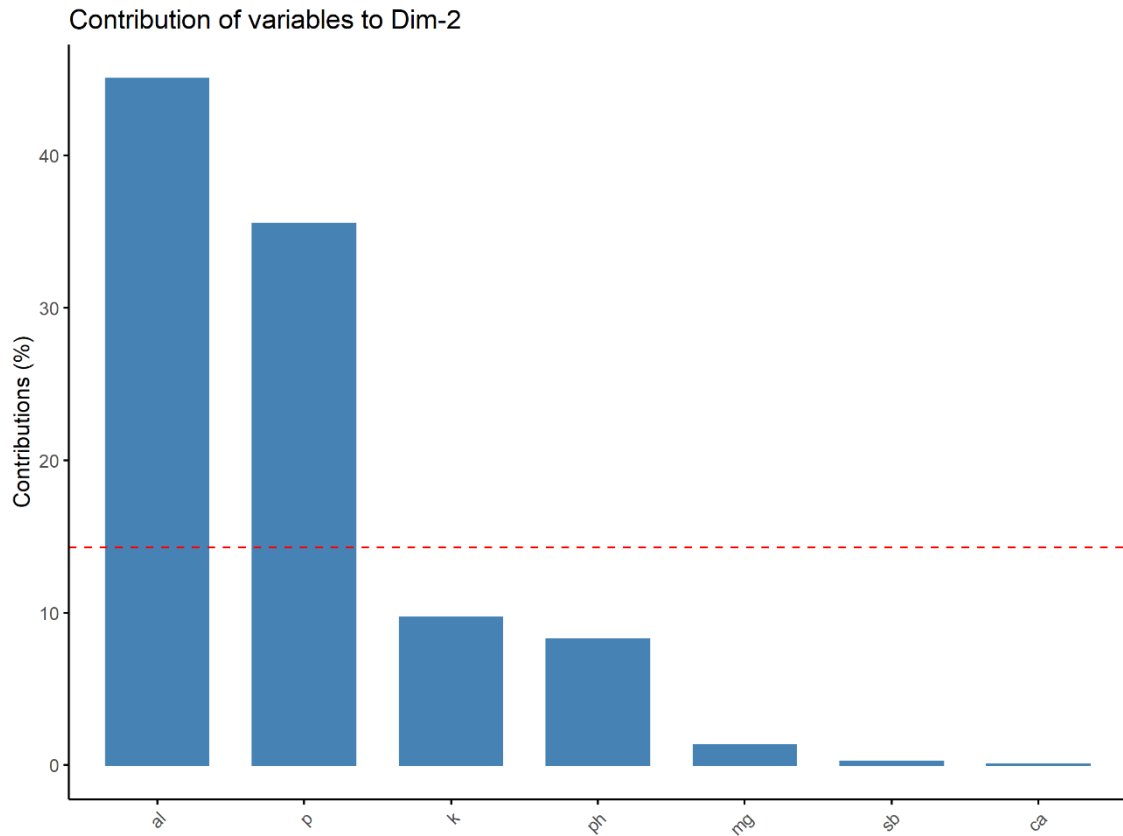


Figure S22. Contribution Plot of Soil Variables to PC2 at Census Level. This contribution plot displays the contribution of seven soil variables—pH (ph), Phosphorus (p), Potassium (k), Calcium (ca), Magnesium (mg), Aluminum (al), and Base Saturation (sb)—to the second principal component (PC2) on the y-axis. The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

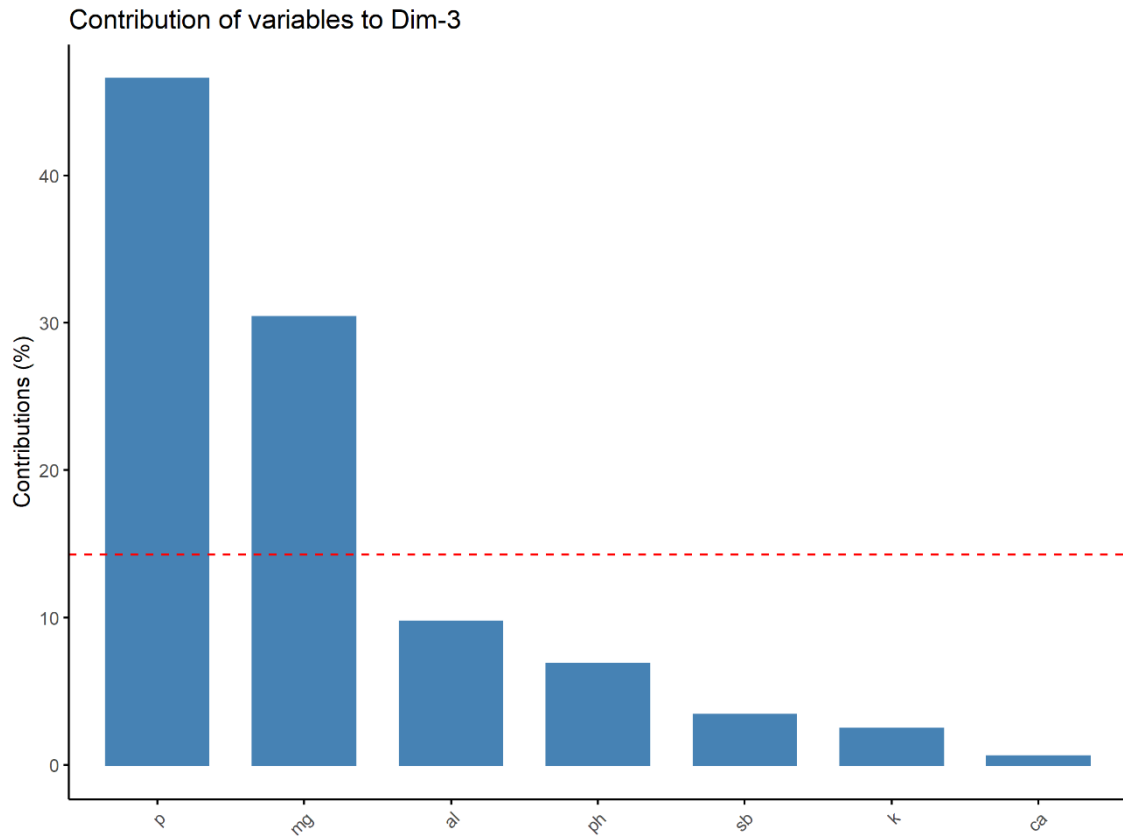


Figure S23. Contribution Plot of Soil Variables to PC3 at Census Level. This contribution plot displays the contribution of seven soil variables—pH (ph), Phosphorus (p), Potassium (k), Calcium (ca), Magnesium (mg), Aluminum (al), and Base Saturation (sb)—to the third principal component (PC3) on the y-axis. The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

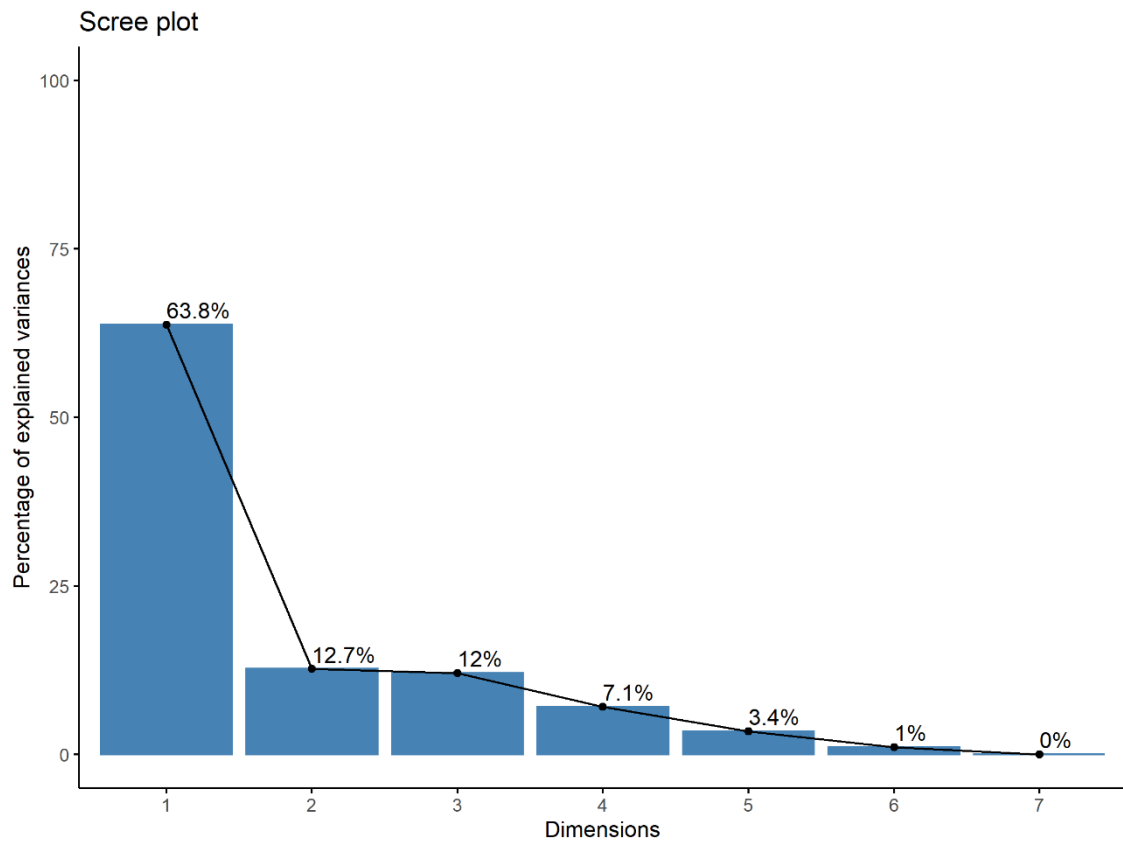


Figure S24. Scree Plot of Principal Components for Soil Variables at Census Level. This scree plot shows the percentage of explained variance of the principal components derived from soil data at the census level. The analysis encompasses data aggregated over complete years within each interval ($n = 163$).

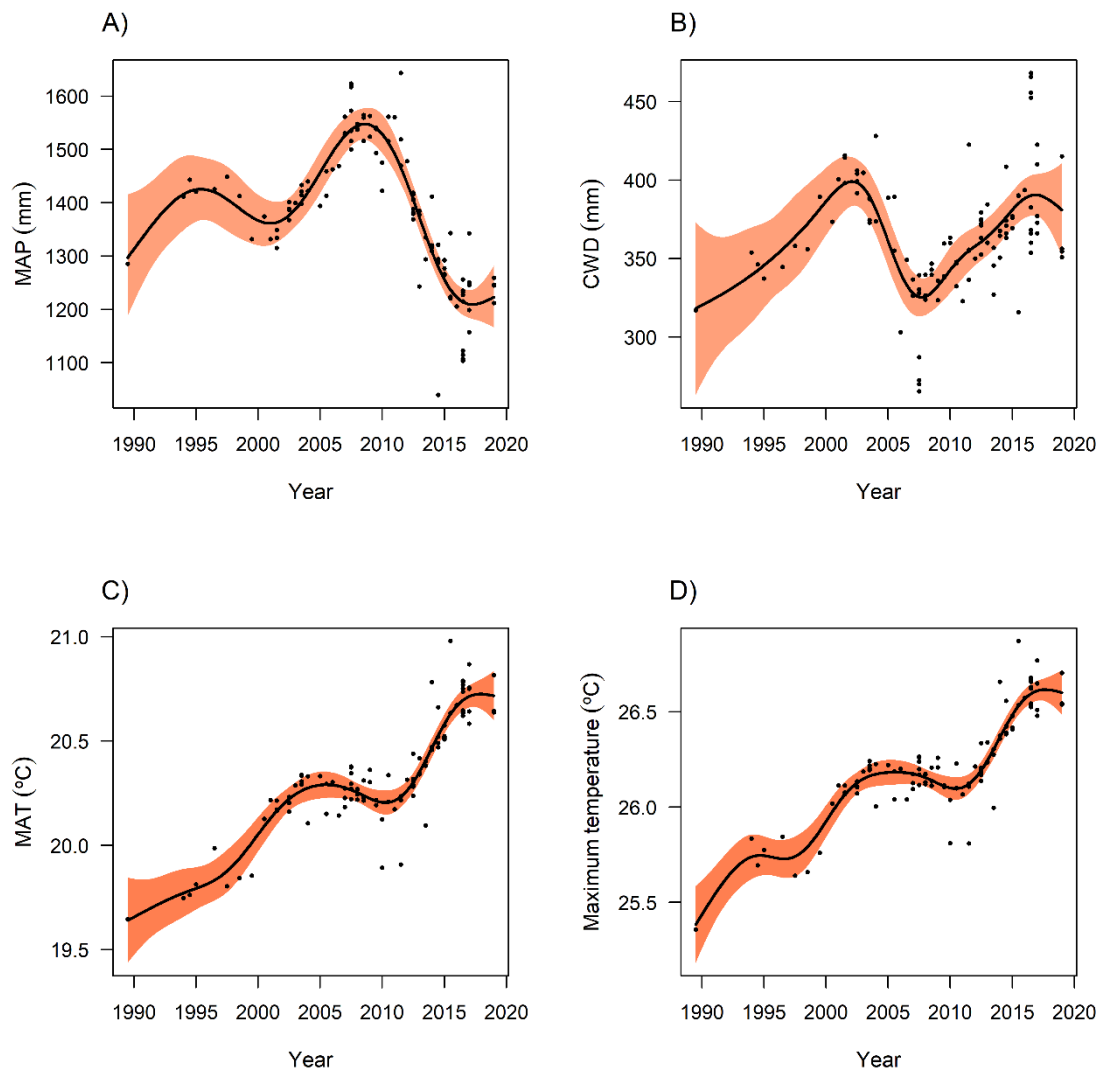


Figure S25. Long-term trends of A) mean annual precipitation (MAP), B) climatological water deficit (CWD), C) mean annual temperature (MAT) and D) maximum temperature. Curves are smooth splines fitted with generalized additive models (GAM). Points are partial residuals (after accounting for the random effect of sites, $n = 49$), corresponding to each census interval ($n = 114$). The shades are the 95% confidence bands of the smooths. Smooth curves with coloured shades were significant at a 95% confidence level, see table 1 for details.

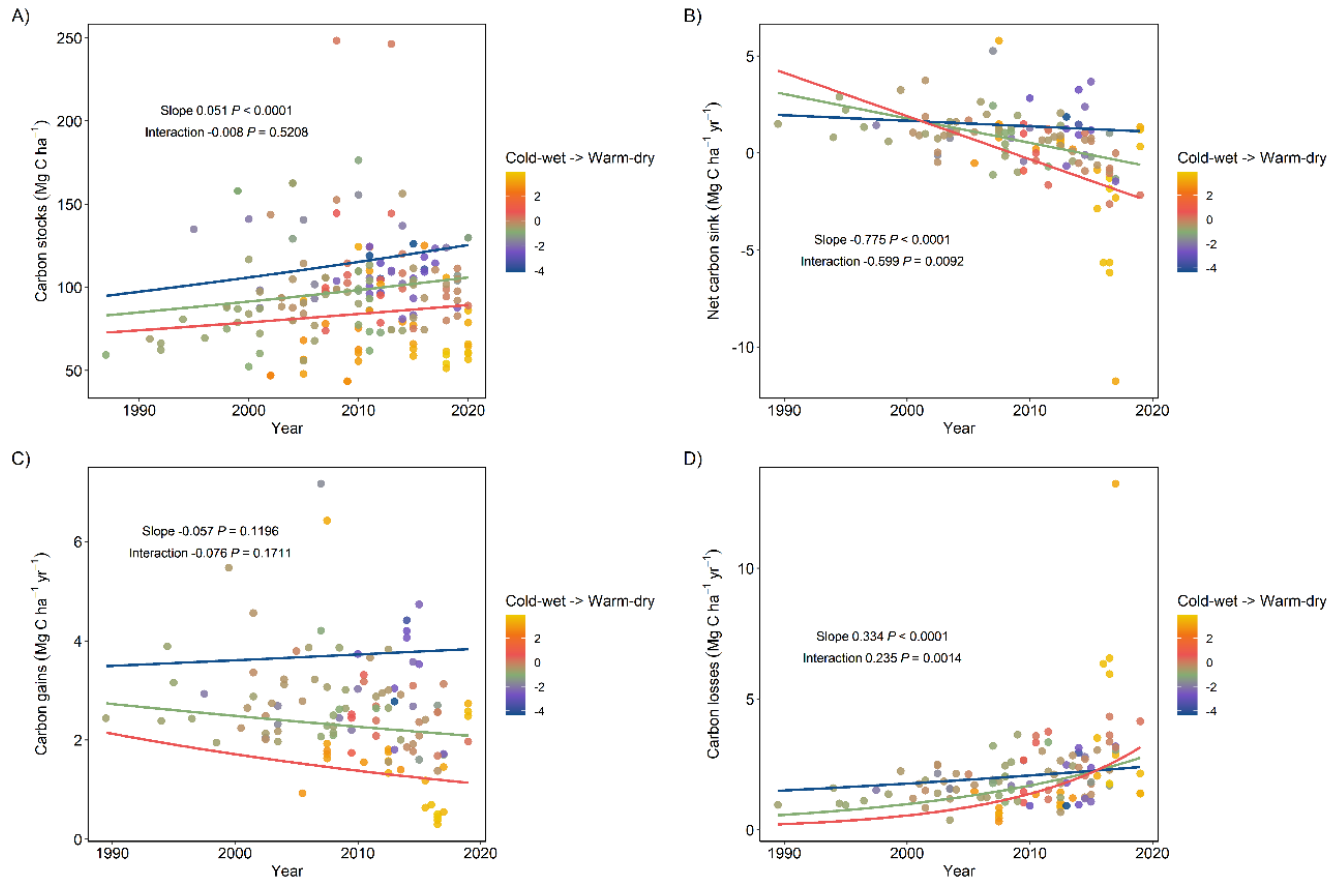


Figure S26. Long-term trends of carbon stocks and dynamics variables on varying levels of climate PCA axis. Points are raw residuals and the curves were fitted with linear mixed-effects models (LMM, including a random effect of site).

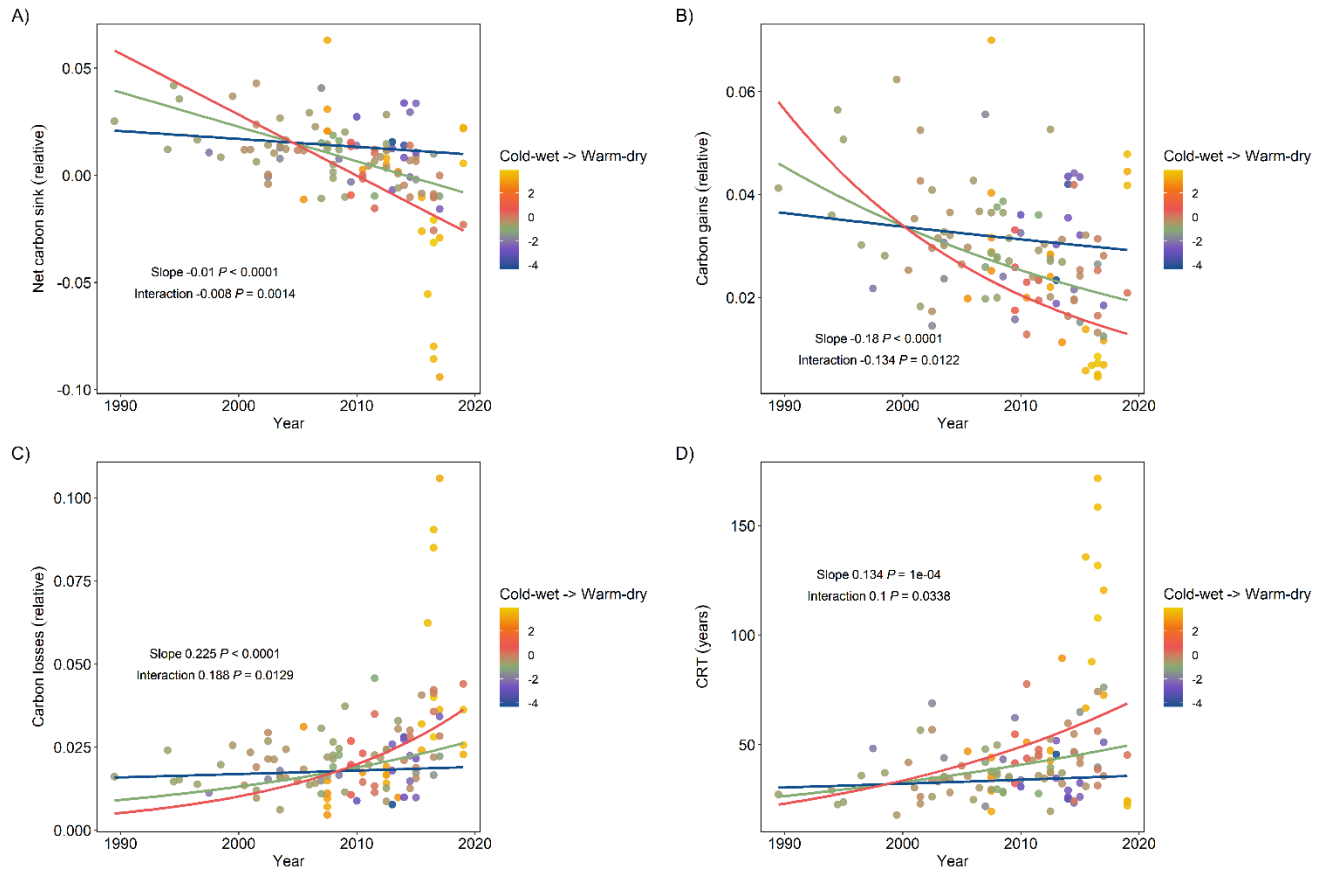


Figure S27. Long-term trends of carbon dynamics variables on varying levels of climate PCA axis. Points are raw residuals and the curves were fitted with linear mixed-effects models (LMM, including a random effect of site).

Supplementary tables

Table S1. Responses variables as a function of time (year) from GAMs. Edf is effective degrees of freedom, F is the F -statistics and the P -value of the smooths.

Response	edf	F	P-value
Carbon stocks	5.645	23.352	0.00000
Net carbon sink	2.88	9.05	0.00001
Net carbon sink (relative)	2.759	11.044	0.00000
Carbon gains	2.253	5.37	0.00397
Carbon gains (relative)	1.385	13.425	0.00003
Carbon losses	2.563	8.765	0.00002
Carbon losses (relative)	3.424	7.174	0.00003
CRT	1	19.951	0.00002
MAP	7.151	40.236	0.00000
CWD	6.902	10.791	0.00000
MAT	7.123	50.652	0.00000
Max. temp	7.624	52.576	0.00000
Taxonomic diversity (Shannon)	2.736	11.92	0.00000
Phylogenetic diversity (PD)	1	19.18	0.00002
WD	3.68	2.09	0.08517
WD dispersion	3.538	6.253	0.00008
SLA	2.957	4.322	0.00374
SLA dispersion	1	7.811	0.00598

Table S2. Multimodel inference results of Carbon stocks. The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with the response variable in the log-scale and centred and scaled predictors.

Carbon stocks (Mg C ha ⁻¹) R ² _{marginal} = 30%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	4.586032	0.038443	0.038729	118.4145	0.000000
Phylogenetic diversity	0.012825	0.020352	0.020502	0.625586	0.531586
Taxonomic diversity	0.071471	0.042669	0.042971	1.663245	0.096263
WD disp	-0.03672	0.034942	0.035186	1.043719	0.296616
Aluminum - phosphorus	-0.03649	0.039166	0.039447	0.925151	0.354887
Phosphorus -> magnesium	-0.08975	0.036742	0.037013	2.424755	0.015319
Site area	-0.01756	0.041381	0.041681	0.421252	0.673571
Soil fertility	0.05411	0.055569	0.055936	0.967357	0.333366
Cold-wet -> Warm-dry	-0.15813	0.042118	0.042413	3.728347	0.000193
Year	0.0508	0.007149	0.007197	7.058742	0.000000
Phylogenetic diversity:Year	0.016014	0.005978	0.006021	2.659671	0.007822
Taxonomic diversity:Year	-0.01223	0.007183	0.007229	1.692557	0.09054
WD disp:Year	-0.0411	0.007409	0.007458	5.510295	0.000000
SLA	0.046778	0.03422	0.034461	1.357419	0.174648
SLA:Year	-0.01283	0.007218	0.007263	1.766776	0.077266
Cold-wet -> Warm-dry:Year	-0.00773	0.01198	0.012045	0.642064	0.520832
WD	0.015591	0.037309	0.037573	0.414958	0.678173
SLA disp	-0.01151	0.027904	0.028087	0.409782	0.681966
SLA disp:Year	0.013069	0.008356	0.008419	1.552325	0.120585
WD:Year	0.008509	0.007058	0.007111	1.196662	0.231439

Table S3. Multimodel inference results of the net carbon sink. The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with centred and scaled predictors.

Net carbon sink (Mg C ha ⁻¹ yr ⁻¹) R ² marginal = 33%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	0.556241	0.145949	0.147695	3.766138	0.000166
SLA	-0.39383	0.206672	0.208607	1.887879	0.059042
SLA disp	0.327199	0.244644	0.246813	1.325697	0.18494
WD disp	-0.46151	0.246593	0.249044	1.853129	0.063864
Aluminum - phosphorus	-0.30183	0.197566	0.19964	1.511888	0.130563
Phosphorus -> magnesium	-0.11036	0.193036	0.195244	0.565237	0.571913
Site area	0.021427	0.190028	0.191892	0.111661	0.911092
Soil fertility	0.69206	0.282155	0.285368	2.425154	0.015302
Cold-wet -> Warm-dry	-0.82286	0.437181	0.440659	1.867328	0.061856
Year	-0.7749	0.161989	0.163893	4.728095	0.0000023
Cold-wet -> Warm-dry:Year	-0.59883	0.227349	0.229909	2.604625	0.009198
WD	0.389411	0.183573	0.185518	2.099051	0.035812
Phylogenetic diversity	0.234202	0.177669	0.179571	1.304234	0.192154
WD disp:Year	-0.37033	0.235098	0.237124	1.561742	0.118349
SLA disp:Year	0.22372	0.17451	0.176505	1.267499	0.204977
Taxonomic diversity	-0.11398	0.208701	0.211066	0.54004	0.589169
SLA:Year	0.012501	0.168626	0.170536	0.073307	0.941562
WD:Year	0.023567	0.215661	0.21824	0.107985	0.914008
Phylogenetic diversity:Year	-0.00716	0.168455	0.170505	0.041985	0.966511

Table S4. Multimodel inference results of the net carbon sink relativized by carbon stocks. The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with centred and scaled predictors.

Net carbon sink (relative) R ² marginal = 35%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	0.006952	0.001554	0.001572	4.42097	0.0000098
SLA	-0.00443	0.002184	0.002205	2.007431	0.044704
SLA disp	0.003312	0.002666	0.002688	1.232307	0.217835
WD disp	-0.00539	0.002751	0.002777	1.9406	0.052307
Aluminum - phosphorus	-0.00266	0.002096	0.002119	1.255337	0.209357
Phosphorus -> magnesium	-0.00149	0.002058	0.002082	0.714577	0.47487
Site area	0.000891	0.001976	0.001996	0.446147	0.655491
Soil fertility	0.006164	0.003015	0.003049	2.021576	0.04322
Cold-wet -> Warm-dry	-0.00639	0.004802	0.004839	1.32068	0.186608
Year	-0.00993	0.001711	0.001731	5.735809	0.000000
Cold-wet -> Warm-dry:Year	-0.00765	0.002361	0.002388	3.204509	0.001353
WD	0.004547	0.002011	0.002032	2.23773	0.025239
SLA disp:Year	0.002913	0.001884	0.001904	1.5295	0.12614
Phylogenetic diversity	0.001633	0.001894	0.001915	0.853021	0.393647
Taxonomic diversity	-0.00152	0.002269	0.002294	0.664017	0.506679
SLA:Year	0.000535	0.001802	0.001822	0.293677	0.769004
WD:Year	-0.00169	0.002374	0.002401	0.705461	0.480523
WD disp:Year	0.00023	0.002395	0.002423	0.094885	0.924406

Table S5. Multimodel inference results of Carbon gains. The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with the response variable in the log-scale and centred and scaled predictors.

Carbon gains (Mg C ha ⁻¹ yr ⁻¹) R ² marginal = 47%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	0.821191	0.032009	0.032379	25.36144	0.000000
WD	0.109238	0.043792	0.044221	2.470261	0.013501
Phylogenetic diversity	0.09953	0.036639	0.037061	2.685593	0.007240
Aluminum - phosphorus	-0.17348	0.039974	0.040428	4.291095	0.0000178
Phosphorus -> magnesium	-0.09045	0.041673	0.042173	2.144802	0.031969
Site area	-0.04015	0.037374	0.0378	1.062143	0.288171
Soil fertility	0.178459	0.060303	0.061019	2.924665	0.003448
Cold-wet -> Warm-dry	-0.49251	0.081006	0.081834	6.018424	0.000000
Year	-0.05675	0.036048	0.03646	1.556456	0.1196
WD:Year	-0.07640	0.044267	0.044788	1.705734	0.088058
Cold-wet -> Warm-dry:Year	-0.07642	0.05527	0.055829	1.368788	0.171066
SLA	-0.04319	0.037424	0.037873	1.140483	0.254085
WD disp	-0.04363	0.057118	0.057748	0.755505	0.449946
Taxonomic diversity	-0.02007	0.043485	0.044003	0.456222	0.64823
Phylogenetic diversity:Year	-0.01168	0.037956	0.038404	0.304098	0.761053
SLA disp	-0.01341	0.044611	0.045116	0.29727	0.76626
WD disp:Year	0.082075	0.048617	0.049213	1.667766	0.095362

Table S6. Multimodel inference results of the carbon gains relativized by carbon stocks. The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with the response variable in the log-scale and centred and scaled predictors.

Carbon gains (relative) R ² marginal = 39%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	-3.66947	0.038732	0.039188	93.63638	0.000000
SLA	-0.14992	0.052763	0.053247	2.815463	0.004871
WD	0.121441	0.048721	0.049206	2.467997	0.013587
Phylogenetic diversity	0.079824	0.047747	0.048221	1.655357	0.097852
SLA disp	0.095463	0.059678	0.060302	1.583076	0.113404
Aluminum - phosphorus	-0.12475	0.049131	0.049691	2.510554	0.012054
Phosphorus -> magnesium	-0.00854	0.048665	0.049227	0.173436	0.862309
Site area	-0.00203	0.049107	0.049611	0.041001	0.967296
Soil fertility	0.137643	0.07057	0.0714	1.927775	0.053883
Cold-wet -> Warm-dry	-0.20691	0.12021	0.121043	1.709429	0.087372
Year	-0.18031	0.038936	0.039374	4.579307	0.0000047
Cold-wet -> Warm-dry:Year	-0.13355	0.052664	0.053269	2.507016	0.012176
WD disp	-0.13672	0.069834	0.070454	1.940613	0.052305
SLA:Year	0.045195	0.039243	0.039706	1.138237	0.255022
SLA disp:Year	0.051895	0.040612	0.041085	1.263106	0.206551
WD:Year	0.022404	0.051674	0.0523	0.428386	0.66837
Taxonomic diversity	0.006681	0.055609	0.056267	0.118735	0.905485
Phylogenetic diversity:Year	-0.02779	0.039892	0.04038	0.688236	0.491304
WD disp:Year	0.00585	0.053378	0.054019	0.108301	0.913757

Table S7. Multimodel inference results of Carbon losses. The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with the response variable in the log-scale and centred and scaled predictors.

Carbon losses (Mg C ha ⁻¹ yr ⁻¹) R ² marginal = 29%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	0.510866	0.04377	0.044294	11.5336	0.000000
SLA	0.131965	0.061065	0.061655	2.140367	0.032325
WD	-0.1085	0.052318	0.052926	2.04999	0.040365
SLA disp	-0.11009	0.064717	0.065441	1.682263	0.092518
Aluminum - phosphorus	-0.07701	0.058791	0.059422	1.295952	0.194992
Phosphorus -> magnesium	-0.09056	0.058841	0.059492	1.522141	0.127974
Site area	0.001013	0.054406	0.054985	0.01842	0.985304
Soil fertility	-0.03795	0.083903	0.08487	0.447111	0.654795
Cold-wet -> Warm-dry	-0.21582	0.117763	0.118901	1.815104	0.069508
Year	0.334201	0.049591	0.05015	6.664074	0.000000
Cold-wet -> Warm-dry:Year	0.234645	0.07289	0.073628	3.18692	0.001438
WD disp	0.067195	0.073984	0.074729	0.899185	0.368554
WD disp:Year	0.153583	0.07378	0.074401	2.064269	0.038992
WD:Year	0.072693	0.078332	0.078927	0.921019	0.357041
Taxonomic diversity	0.024848	0.060733	0.061446	0.404391	0.685925
SLA disp:Year	-0.02069	0.049232	0.049835	0.415181	0.67801
Phylogenetic diversity	0.024858	0.051936	0.052519	0.473324	0.635982
SLA:Year	0.002476	0.048033	0.048612	0.050937	0.959376

Table S8. Multimodel inference results of the carbon losses relativized by carbon stocks. The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with the response variable in the log-scale and centred and scaled predictors.

Carbon losses (relative) R ² marginal = 18%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	-3.98086	0.042528	0.043025	92.52469	0.000000
Aluminum - phosphorus	-0.03059	0.051454	0.052049	0.587734	0.556711
Phosphorus -> magnesium	-0.02657	0.054076	0.054705	0.485619	0.627237
Site area	0.015773	0.045683	0.046228	0.341209	0.732946
Soil fertility	-0.07717	0.078875	0.0798	0.96709	0.333499
Cold-wet -> Warm-dry	0.042482	0.107756	0.108917	0.390043	0.696505
Year	0.225384	0.050224	0.050743	4.441692	0.0000089
Cold-wet -> Warm-dry:Year	0.187986	0.074952	0.075633	2.485514	0.012937
WD	-0.10048	0.059499	0.0601	1.67181	0.094562
WD:Year	0.14383	0.068797	0.069407	2.072259	0.038241
WD disp	-0.00925	0.070357	0.071179	0.129889	0.896655
WD disp:Year	0.137956	0.05945	0.060074	2.29642	0.021652
Phylogenetic diversity	0.012294	0.048608	0.049146	0.250152	0.80247
Taxonomic diversity	0.024991	0.056435	0.0571	0.437679	0.661619
SLA disp	-0.00591	0.052127	0.052726	0.112086	0.910755
SLA	0.016778	0.047992	0.048563	0.345493	0.729724
SLA:Year	0.055728	0.04616	0.046714	1.192951	0.232889
Taxonomic diversity:Year	0.064964	0.058271	0.058971	1.10162	0.270627

Table S9. Multimodel inference results of carbon residence time(CRT). The estimate is the conditional averaged coefficient followed by its standard error and *P*-value. The models were fitted with the response variable in the log-scale and centred and scaled predictors.

CTR R ² marginal = 34%					
Predictor	Estimate	Std. Error	Adjusted SE	z value	Pr(> z)
Intercept	3.701483	0.033644	0.034026	108.7851	0.000000
SLA	0.132979	0.043252	0.04368	3.044409	0.002331
WD	-0.10002	0.042333	0.04275	2.339773	0.019296
Aluminum - phosphorus	0.11518	0.042804	0.043285	2.660973	0.007792
Phosphorus -> magnesium	0.004586	0.042202	0.042688	0.107434	0.914445
Site area	-0.01843	0.042649	0.043081	0.427696	0.668873
Soil fertility	-0.11078	0.061286	0.062	1.786748	0.073978
Cold-wet -> Warm-dry	0.179405	0.106382	0.107066	1.675647	0.093807
Year	0.13372	0.034849	0.035226	3.796105	0.000147
Cold-wet -> Warm-dry:Year	0.09971	0.046434	0.046969	2.122919	0.033761
WD disp	0.113765	0.059223	0.059764	1.903594	0.056963
Phylogenetic diversity	-0.07223	0.039967	0.040377	1.788915	0.073629
SLA disp	-0.07131	0.051399	0.051946	1.372775	0.169823
SLA:Year	-0.04127	0.034302	0.034709	1.188986	0.234445
WD:Year	-0.02202	0.047545	0.048046	0.458265	0.646762
SLA disp:Year	-0.03859	0.036212	0.036622	1.053613	0.29206
Phylogenetic diversity:Year	0.023482	0.035215	0.035641	0.658849	0.509993
Taxonomic diversity	-0.00135	0.047397	0.047955	0.02815	0.977543
WD disp:Year	0.018913	0.05051	0.050958	0.371136	0.710536
Taxonomic diversity:Year	-0.06189	0.037296	0.037753	1.639336	0.101143